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Proceedings of the
International Large River Symposium (LARS)

Edited by:

Douglas P. Dodge

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Proceedings of the International Large River Symposium (LARS)

(Honey Harbour, Ontario, Canada, September 14–21, 1986)

Edited by
Douglas P. Dodge

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The LARS Logo

The LARS logo is a semi-abstract representation of a fish, half hidden by the waves of a large river, beneath the sun and the sky. The design is an interplay between four elements: fish, water, sky, and man; a recognition of man's place in the ecosystem and the interdependence of these elements, to the benefit of each. The relationship of the fish and the large river is suggested by the repetition of the "flow" motif in both fish and river; they are a part of each other. The presence of sun and sky complements this cycle. Most important is man's role in this cycle, as represented by the letters reaching down into the waters of the large river making the picture of this mutually beneficial ecosystem complete.

Paul Pascal, *Designer*

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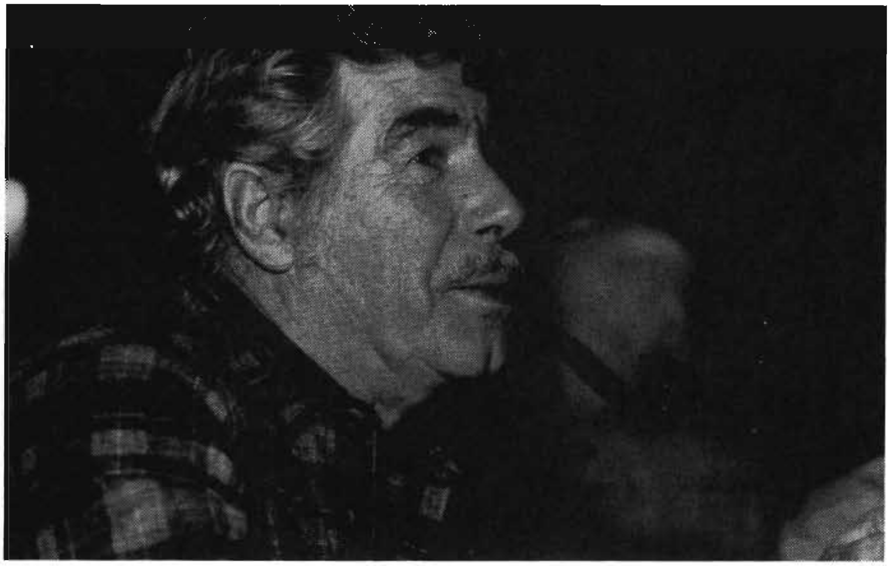
Dedication — LARS

Kenneth H. Loftus created a tradition of scientific excellence in Ontario exemplified by the SCOL (Salmonid Communities in Oligotrophic Lakes) Symposium of 1971, which continued through several subsequent symposia to the most recent, the Large River Symposium (LARS) of which he was an active participant. He established a collegial and interactive procedure for these symposia that has resulted over the years in the promulgation of a wealth of good science, and subsequently, successful science transfer to the resource user. In the ensuing years, this tradition has been a notable feature of Ontario-sponsored symposia.

The gratitude of the LARS participants for the philosophical and ecological legacy left by Ken Loftus is unbounded. Accordingly, we respectfully dedicate this volume of the Large River Symposium to his memory.

[*Ken Loftus passed away on April 10, 1988, at Richmond Hill, Ontario*].



Introduction to the International Large River Symposium (LARS)

Douglas P. Dodge and Deborah L. Conrad

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The International Large River Symposium (LARS) was organized to increase our understanding of large river management for fish production. A special effort to address the complexities of fish production and management in large rivers was needed because the world demand for protein is steadily increasing pressure on fish stocks. At present, approximately half of the annual world catch of commercial fish (≈5 million t) comes from running water and adjacent floodplains. As well, approximately 20% of the sport fishery in North America occurs on rivers and streams, and in South America, more than 70 million fish are harvested annually for sale as ornamental species.

Despite their recognized importance for fish, rivers worldwide are being subjected to increasing demands for water supplies, flood control, transportation, irrigation and energy production, all of which usually adversely affect the production of fish and other aquatic life. In North America, large rivers are constantly in jeopardy from proposals for large scale diversions (Gamble 1987). Concomitantly, exploitation has also contributed to the disappearance and decline of local fish stocks in some countries. Unfortunately, fisheries management of rivers has remained relatively unchanged for several decades, especially for river inventory and methods standardization, for the estimation of productivity and for the setting of allowable harvests.

In response to these issues, the Ontario Ministry of Natural Resources initiated LARS. The main objectives of LARS were:

1. To produce reliable estimators of fish yield by:
   a) reviewing existing estimators of production and standing stocks in large rivers and
   b) summarizing current river inventory and assessment techniques for biotic and abiotic variables
2. To publish the case studies and synthesis papers
3. To identify areas requiring further study to improve river resource management and
4. To improve communication and liaison between scientists in research and management, university and government.

LARS used the same organizational structure as SCOL (Loftus and Regier 1972), PERCIS (Colby 1977), and STOCS (Berst and Simon 1981). A series of overview and case history papers were presented. Each overview paper examined recent science of river management and research, emphasizing theoretical constructs and ecological insights. Each case history paper presented historical information on a particular major river system. These two sets of papers formed the background for the synthesis process that followed.

Subsequently, five working groups examined (1) the transfer of science between researchers, managers and the public (Biette et al. 1989), (2) the management of fish populations (Petts et al. 1989), (3) the procedures for sampling fish populations (J.M. Casselman, Ontario Ministry of Natural Resources, Lake Ontario Fisheries Unit, RR #4, Picton, Ont. K0K 2T0, personal communication), (4) the incorporation of biosocioeconomic issues into fisheries management (Malvestuto 1989), and (5) the assemblages of fish in river systems (Welcomme et al. 1989). The LARS symposium brought together 80 experts on large river management from 15 countries and created a forum in which to exchange ideas, and ultimately to recognize that fundamental problems with large river systems are similar throughout the world.

Acknowledgements

Many people contributed to the successful completion of this symposium. We extend special thanks to the other members of the Steering Committee: Raymond M. Biette, Chris S. Brousseau, Gareth A. Goodchild, R. Mac Odell, Richard A. Ryder, and Robin L. Welcomme. We also acknowledge the Editorial Board, comprised of the Steering Committee as well as George R. Spangler and the late Kenneth H. Loftus.

We acknowledge the support of the Ontario Ministry of Natural Resources, Fisheries Branch staff, especially Bluebell Fernandez, Dennis Stann, Jack Imhof, Gerry Smitka, Marisa Succi, Erika Thimm, and Nargis Valli. Marusia Borodacz, in-house librarian, provided excellent support for the synthesis groups, and Gordon Whitehead drafted many of the figures for the publication. The symposium was strongly supported by A.S. Holder, former Director of Fisheries Branch, who committed staff and funds for this endeavour. Cheryl Goodchild prepared the Appendix.

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References

Berst, A. H., and R. C. Simon. 1981. Proceedings of the 1980 Stock Concept International Symposium (STOCS). Can. J. Fish. Aquat. Sci. 38: 1457–1921.

Biette, R. M., G. A. Goodchild, and S. J. Nepszy. 1989. Science transfer networks for large river management, p. 600–606. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Colby, P. J. 1977. Proceedings of the 1976 Percid International Symposium (PERCIS). J. Fish. Res. Board Can. 34: 1447–1999.

Gamble, D. J. 1987. The Grand Canal and the National Interest: When Should Rational Thinking Apply to Water Policy? Northern Perspectives 15 (3): 2–7.

Loftus, K. H., and H. A. Regier. 1972. Proceedings of the 1971 Symposium on Salmonid Communities in Oligotrophic Lakes (SCOL). J. Fish. Res. Board Can. 29: 611–986.

MALVESTUTO, S. P. 1989. Sociological perspectives on large river management: a framework for application of optimum yield, p. 589-599. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

PETTS, G. E., J. G. IMHOF, B. A. MANNY, J. F. B. MAHER, AND S. B. WEISBERG. 1989. Management of fish populations in large rivers: a review of tools and approaches, p. 578-588. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

WELCOMME, R. L., R. A. RYDER, AND J. A. SEDELL. 1989. Dynamics of fish assemblages in river systems — a synthesis, p. 569-577. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Introduction of Professor H. B. N. Hynes

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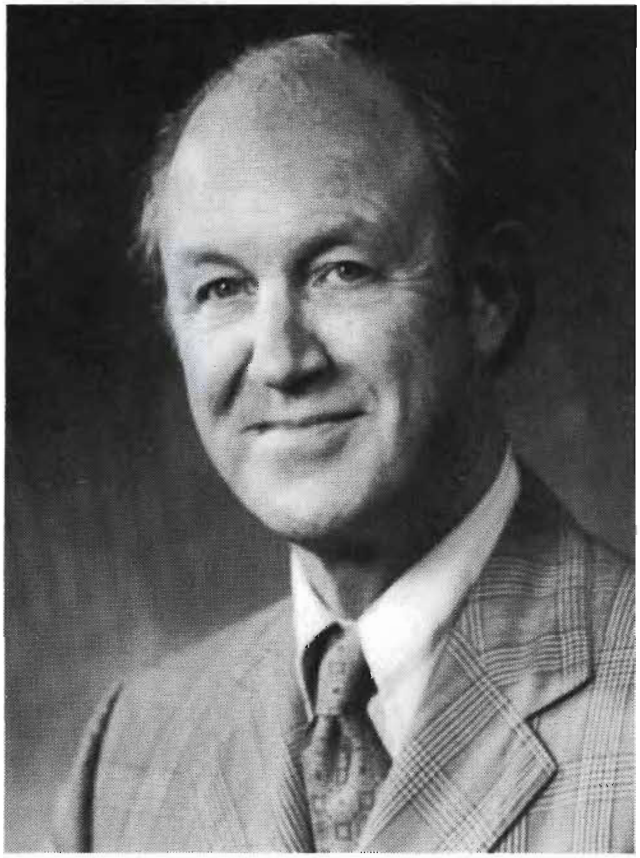

H.B.N. Hynes

It is my distinct pleasure to introduce Noel Hynes, whom I regard as the world's foremost running water ecologist.

Dr. Hynes, Professor Emeritus of Biology at the University of Waterloo, Ontario, was awarded the Ph.D. degree in 1941 from the University of London. His doctoral research dealt with stoneflies (Plecoptera), the most rheophilic order of aquatic insects.

After his time as a graduate student at the Freshwater Biological Association Laboratory at Windermere, Dr. Hynes worked on tropical agriculture in the West Indies and on locusts in Africa. He was eventually put in charge of the locust program for the Somali Horn of Africa. His first love, running waters, was not forgotten, however, and he somehow managed to continue research on aquatic systems and their inhabitants even during those early years.

Dr. Hynes returned to the United Kingdom in 1946 to join the Faculty of Zoology at the University of Liverpool. He completed requirements for the D.Sc. degree from the University of London in 1958. In 1964 he emigrated to Canada to accept a post at the University of Waterloo where he stayed for the remainder of his career. He retired from teaching in 1983.

Professor Hynes has a truly global perspective, having conducted research not only in the British Isles, Africa and the West Indies, but also in various parts of Continental Europe, Canada, the United States, Australia, and Tasmania. His former students are scattered over four continents.

During a remarkably productive career, Prof. Hynes' research has ranged from organismic to ecosystem levels of organization, and has included a variety of topical areas (taxonomy, phylogeny, morphology, embryology, parasitology, toxicology, behavior, zoogeography, and ecology). He has worked with many groups of organisms, with an emphasis on stoneflies, gammarid amphipods, black flies, and sticklebacks. He has contributed significantly to our understanding of running waters in a wide variety of topics (Table 1).

TABLE 1. Some research foci of H. B. N. Hynes.

Trophic Dynamics
River Pollution
Organic Matter Processing
Aquatic Productivity
Hyporheic Fauna
Role of Dissolved Organics
Stream Recolonization
Groundwater Hydrology
Micro — and Macrodistribution
Life History Phenomena
Symbiotic Relationships
Water Quality Indicators

His first book, *The Biology of Polluted Waters* (Hynes 1960), in my opinion still presents the best overall account of the subject. But the impact of his second book, *The Ecology of Running Waters* (Hynes 1970), published a decade later, was even greater. In addition to being well written and illustrated, this book summarized the extant world literature on running water ecology. The depth and breadth of Prof. Hynes' influence is further exemplified by a 1981 book, *Perspectives in Running Water Ecology* (Lock and Williams 1981), dedicated to him by former students and postdoctoral fellows, many of whom contributed chapters.

Professor Hynes has published 177 papers at last count. Those that I feel have had a particularly great impact on the field are listed in Table 2. "The Stream and its Valley", based on the Baldi Lecture presented at the Nineteenth International Congress of Limnology held in Winnipeg, perhaps best exemplifies, in succinct form, Noel Hynes' holistic perspective of running waters. Not only did this paper contribute greatly to the acceptance of lotic ecology as a legitimate

TABLE 2. Some seminal papers by H. B. N. Hynes.

1941.	The taxonomy and ecology of the nymphs of British Plecoptera. Trans. R. Entomol. Soc. Lond. 91: 459–557.
1950.	The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. J. Anim. Ecol. 19: 35–38.
1961.	The invertebrate fauna of a Welsh mountain stream. Arch. Hydrobiol. 57: 344–388.
1968.	A simple method of assessing the annual production of stream benthos. Limnol. Oceanogr. 13: 569–573 (with M. Coleman).
1970.	The vertical distribution of the invertebrate fauna in the bed of a stream. Limnol. Oceanogr. 15: 31–40 (with M. Coleman).
1971.	The fate of the dead leaves that fall into streams. Arch. Hydrobiol. 68: 465–515 (with N. Kaushik).
1975.	The stream and its valley (Baldi Lecture). Verh. Int. Verein. Limnol. 19: 1–15.
1983.	Groundwater and stream ecology. Hydrobiologia 100: 93–99.

branch of limnology, it also recognized the catchment as a component of the running water ecosystem.

One could go on, but in conclusion I must say Prof. Hynes' most important contribution is the tremendous influence that he had on the thinking of students of lotic ecology. No one individual has made a greater impact in that regard.

I now turn over the podium to Prof. H.B.N. Hynes.

References

HYNES, H. B. N. 1960. The biology of polluted waters. University Press, Liverpool. 202 p.

1970. The ecology of running waters. University of Toronto Press, Toronto, Ont. 555 p.

LOCK, M. A., AND D. D. WILLIAMS [ed.]. 1981. Perspectives in running water ecology. Plenum Press, New York, NY. 430 p.

Keynote Address

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Abstract

HYNES, H. B. N. 1989. Keynote Address, p. 5–10. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Only about 0.4 % of the literature dealing with the ecology of running waters is concerned with large rivers, even though some of the very early papers were about them. During the past century man has for the first time begun to have effect on large watercourses, and he has very quickly degraded almost all of them by engineering for navigation, water and power supply, pollution and alterations of land use.

Serious study of running-water biology postdates nearly all this development, so we have little time left in which to find out how the large river biotic community functions, and without that knowledge we are unlikely to be able to manage large rivers effectively to our advantage.

At present we are operating on the assumption that we can extrapolate from our knowledge of small watercourses, obtaining by using very simple apparatus, to larger ones. This is probably not entirely valid, and it has already been found out, by ingenious use of simple apparatus and bright ideas, that the large river habitat is a very complex one. We also know that ''snag'' habitats, which are extremely difficult to sample with current apparatus, and which are often the first targets for removal by engineers, are very important to productivity in big rivers, and may play a large role in the lives of important fish species.

It is suggested that we should be less ready to indulge in management practices, such as introductions of alien species, until we are better informed, and that this better information is going to involve using complex and heavy apparatus; and it will be costly. The analogy is drawn between large river ecology and marine science, which took off only when big money was spent upon it. The oceans, however, remain relatively unaltered; the need to study the changing and already despoiled rivers is very urgent.

Résumé

HYNES, H. B. N. 1989. Keynote Address, p. 5—10. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium, Can. Spec. Publ. Fish. Aquat. Sci. 106.

Seuls environ 0,4 % des ouvrages publiés sur l'écologie des eaux courantes portent sur les grands cours d'eau, même s'ils ont fait l'objet des premières études scientifiques. Au cours du dernier siècle, l'influence de l'homme sur les grands cours d'eau s'est fait sentir pour la première fois ; ses activités dans le domaine du génie naval, de l'alimentation en eau et de la construction de barrages ainsi que des modifications de l'utilisation des terres et la pollution connexe ont rapidement altéré la plupart d'entre eux.

D'importantes études sur la biologie des eaux courantes n'ont été effectuées qu'après la réalisation de la plus grande partie de ces projets. Nous ne disposons donc que de peu de temps pour découvrir comment la grande communauté biotique fluviale fonctionne car sans ces connaissances, il est fort peu probable que nous saurons comment gérer efficacement les grands cours d'eau.

Nous nous fondons actuellement sur l'hypothèse que nos connaissances sur les petits cours d'eau peuvent être extrapolées pour en déduire des hypothèses sur les grands cours d'eau. Il est probable que ceci ne soit pas entièrement valable car on a déjà découvert, par l'utilisation ingénieuse d'appareils simples et l'application d'idées brillantes, que l'habitat créé par les grands cours d'eau est très complexe. Nous savons aussi que les habitats créés par les écueils, très difficiles à échantillonner à l'aide des appareils courants et qui sont souvent les premières cibles des ingénieurs, sont très importants pour la productivité des grands cours d'eau et peuvent jouer un rôle primordial dans le cycle vital d'importantes espèces de poissons. Avant d'appliquer certaines pratiques de gestion, comme l'introduction d'espèces non indigènes, on devrait obtenir des données pertinentes qui ne pourront être recueillies qu'à l'aide d'appareils complexes et dispendieux. On peut établir un parallèle entre l'écologie des grands cours d'eau et les sciences marines qui n'ont pris de l'essor qu'au moment où de fortes sommes ont été dépensées. Toutefois, les océans sont demeurés relativement intouchés, ce qui n'est pas le cas des grands cours d'eau. Il est donc urgent d'étudier les milieux fluviaux en phase d'évolution et ceux déjà dégradés.

Introduction

In opening this symposium, Dr. Dodge stressed that we know very little about large rivers which he defined as those large enough to intimidate research workers. R.T. Milhous (see Stalnaker et al. 1989) agreed with his definition, which is the best one that I have yet heard. Ecological definitions are always difficult, but among the approximately 10 000 scientific articles dealing with ecological topics associated with running water that I know about, a few more than 400 are concerned to some extent with large rivers. That would seem to be a reasonable proportion; but, as I hope to confirm, our knowledge of larger rivers lags far behind that of smaller streams, and we still have a very long, and probably expensive, way to go before we can say that we even begin to understand them.

Large rivers have always been of importance to mankind as routes within the interior, as fishery resources and as general amenities; and during the present century we have come to the idea that perhaps we should be managing them better. Indeed, my letter of invitation to address this symposium mentioned some topics that I might deal with, and among the seven that were listed, four were to do with management. I believe that we are not very good managers simply because we do not know enough.

Historical Considerations

Before the industrial revolution, mankind did little to alter large rivers; they were too large to dam, and they contained too much water to pollute before the invention of the flush toilet and big industry. So they were used mainly for navigation and fishing, and people put up with any inconveniences presented by floods, rapids and waterfalls. For instance, throughout classical Egyptian history, the cataracts on the Nile were trans-shipment points, and they must have cost enormous numbers of hours of labour. Nowadays at Aswan, one may still see the First Cataract, which probably remains there only because it is below a large impoundment and so is in nobody's way. Had there been an Ancient Egyptian Corps of Engineers, the cataract would long ago have been replaced by a low-head dam and some lock gates, just like the similar irritating barrier to navigation on the Ohio at Louisville, Kentucky.

Much of the navigational and chemical alteration of rivers was well under way before any studies on their ecology began, although it is interesting to note that two of the very earliest limnological papers do indeed deal with large rivers (Lauterborn 1893; Zacharias 1898), even before Thienemann began his classical studies on small streams at the turn of the century. This interest in large rivers persisted for some years before the easier work on smaller streams took over. Lauterborn (1916), however, continued his studies ont the Rhine, and Behning (1928) worked on the Volga. Theirs are valuable papers as they precede at least some of the alterations of the Rhine, but the corresponding North American work (Richardson 1921) dealt primarily with pollution of the Illinois River, so here, in North America, we have even less information than do the Europeans. Even the connecting channels of the Great Lakes have, as Edwards et al. (1989) have stressed here, been little studied from a biological point of view until recently.

Early studies were performed with the minimum of apparatus; it is apparent that the same lack of concerted effort on river investigations persists even today. One becomes aware of this when looking through the various monographs on large rivers that have been published in recent years, such as Liepolt (1967)on the Danube, Mordukhai-Boltovskoi (1979) on the Volga, Rzoska (1976, 1985) on the Nile and on the Niger, Sioli (1984) on the Amazon, Whitton (1984) on European rivers, and Davies and Walker (1986) on many rivers all over the planet. These books describe studies that have been done to a large extent on an *ad hoc* basis, with borrowed boats, improvised apparatus, and very often without much continuity. The only data that are fairly good, and that is true for only some rivers, are fishery statistics; but they are at best a very crude estimate of the totality of ecological conditions in a large body of running water.

Marine biology went through a rather similar phase during the period between the two world wars. I well remember senior biologists in the thirties talking scornfully about "rubber-boot" oceanography (they called it marine biology), and how it would become possible to understand the seas, and to manage the fisheries, only if much more effort and money were put into their study. Today's oceanography shows that a better funded approach has paid off, and marine scientists were fortunate that their intensive, well-equipped work began well before mankind really started to affect the oceans.

In contrast, very few large rivers are left for study in anything like their original condition, so, as Ward and Stanford (1989) have also stressed here, it is very difficult to know what many of them were like in their pristine state. In Asia, Australia and Europe, there are probably none now in pristine condition, with the possible exception of northern Siberia, but even there, dams and flow reversals are being planned or implemented. In Africa, the Zaire is still not much altered (Davies and Walker 1986), in South America, the Amazon has so far survived without too many drastic changes (Sioli 1984), and in North America the Mackenzie is not yet much damaged. But all of these are threatened with development: Amazonian forests are being cleared, the Zaire is a potential source of electrical power, and also offers the best prospects for transportation within its vast basin, and the Mackenzie lies in an area that is threatened with petroleum development, involving huge pipeline routes along the valley (Davies and Walker 1986). Already the Athabasca, a major tributary of the Mackenzie, flows precariously across a vast area of oil-sands mining (Barton and Lock 1979), and it has been involved in blackfly control further upstream (Haufe and Croome 1980; Fredeen 1983); the Peace River, another major tributary, has been dammed for electricity generation.

So there really is little time left, and soon almost all large rivers will have histories of alteration and change, almost always for the worse, such as may be read in Whitton's (1984) book on European rivers, and Davies and Walker's (1986) on many other rivers elsewhere. I find Boyle's popular book on the Hudson River (1979), written by a man who really loves his subject, a particularly poignant account of such an evolution.

The Current Situation

Our present knowledge of the biota of large rivers suffers from the fact that, apart from the few examples cited above, almost all serious study has been undertaken long after the effects of human alteration had become severe. We have anecdotal accounts of such things as a swift clearwater primordial Ohio River and a silt-laden Missouri, which now runs clear because of mainstem dams. We also know that the fish fauna of many rivers has changed considerably in recent times, but very often we do not have real understanding of the causes of biological changes. One possible exception applies to tropical floodplain rivers where damming reduces the spawning activities of fishes by keeping their spawning sites dry during rainy seasons (Welcomme 1980, 1985). But even there we have little information on the effects of such alterations on invertebrates and plants, and hence on the general productivity and ecological robustness of the ecosystem.

Even in Europe, with its long history of amateur biology, the old records are more tantalizing than informative. We know for instance that some large river inhabitants have disappeared or become very scarce. Zwick (1980) lists several species of stonefly that seem to be extinct or almost so. I well remember being very intrigued by a late nineteenth century record of a stonefly, of the family Perlodidae as was quite certain from the brief description, from a bridge across the Thames in London at a point where no stonefly could live nowadays, and most certainly not when I was a graduate student. I suspect that it was *Isogenus nubecula*, now almost absent from Europe, but at one time a common inhabitant of the Rhine and the Danube at Vienna. This was a large river species which survives today only in the short lowest reaches of fairly small rivers that are not much altered. It is therefore under constant threat. I found it 25 years ago in a short stretch of the River Dee on the Welsh boundary, probably one of its final strongholds in Britain. I wonder if it is still there, now that the upper reaches of that river have been extensively impounded to supply water to Liverpool. The response of the average person would, I am sure, be to ask who cares about a stonefly. My response is that we all should do so, because it is a symptom of environmental health.

I also wonder if the report of Sanders and Bingham (1981) of the finding of two rare species of Ephemeroptera in the lower Mississippi River is not another example of the precarious survival of large river species which are rare only because man has altered most of their original habitat. A fascinating group of highly specialized fishes that seems to be at future risk is the one that has evolved in the lower rapids of the Zaire River (Roberts and Stewart 1976). Doubtless even very little in the way of development of that river, which seems inevitable, will remove that fauna for ever. We have also heard here of the threatened status of the very highly adapted community of fastwater fish in the Colorado River (Carlson and Muth 1989). One wonders how many other such biota had disappeared before they were even discovered by science.

We may be grateful that there was not an Ancient Egyptian Corps of Engineers, but, not long after that possibility, the Romans became fairly good at controlling the flow of water. They also introduced species all over the place. We know, for instance, that they carried the Asian carp (*Cyprinus carpio*) throughout Europe. It became so entrenched there that North Americans usually call it the European or German carp, but we have no records of its effect on the original biota. In more recent times, when we have also foolishly carried this fish to other continents, we have produced very undesirable results. In North America, most such effects have been noted in still waters — go and look at Lake Erie or even beautiful Georgian Bay — but in Australia a large watercourse is badly affected, as is apparent from accounts of the Murray River (Davies and Walker 1986), where another alien fish, *Gambusia affinis*, is also causing problems by outcompeting native species.

There are convincing indications that threats to the specialized fishes of the Colorado River are at least in part caused by the introduction of alien species, yet people still persist with suggestions of introductions of so-called "desirable" species in the name of fishery management. That is a measure of their ignorance, their narrowness of thought and their disregard of the mess that, for example, has been made of the St. Lawrence system by repeated introductions of alien fishes with no real understanding of the consequences. It is a symptom of the persistence of this ignorance that some Australian fishery people are advocating the introduction of *Lates niloticus*, the Nile perch, into northern Australian rivers, because it is in the same genus as their delicious barramundi, but it breeds in fresh water, which the barramundi does not. *Lates niloticus* is certainly a very good fish to eat, but when it has been introduced into African waters in which it did not previously occur it has behaved like a fox in a chicken-run.

Other causes of change in large rivers are pollution and land use. The first is perhaps too obvious to merit more than a mention; however, it should not be forgotten that pollution is often cumulative, and that the large river is the ultimate sink into which everything that is not broken down upstream ultimately flows. I believe we have as yet far too little understanding of the second; land use has enormous effects on running water, and again the large river is the ultimate freshwater sink. Erosion, deforestation, afforestation, urbanization, irrigation and many other such activities must alter large rivers in ways that we do not understand. If we really did comprehend these effects we could use large rivers to monitor the ecological health of the whole of their drainage basins, and that would be of enormous benefit to us all.

I have already mentioned navigation and the changing of most large rivers into a series of pools separated by dams with lock gates. This is now almost universal in Europe and North America, so the original large-river habitat has almost disappeared. Perhaps in such rivers as the Thames, the Mississippi, the Columbia and the Ohio, we should be thinking in terms of riverine lakes rather than rivers. But many, probably most, rivers have been impounded with much bigger dams in recent decades, and this is an activity that continues at an increasing pace. Its effects are enormous, and cannot be dealt with in any detail here. They include alterations in flow and temperature regimes, changes in patterns of sediment removal and accrual, reductions in total discharge and hence, very often, increases in total dissolved solids. All these changes, and others, produce effects on the biota (see Ward and Stanford 1979; Lillehammer and Saltveit 1984). Some particularly important effects are inhibition of migration of fishes, alterations in life cycles because of temperature changes, the floodplain desiccation mentioned above, and, in USSR, the spread far south, down rivers such as the Volga, of species that were originally northern in distribution.

Possible Ways Ahead

A major problem until quite recently has been that the ecology of flowing water has been very difficult to conceptualize. Rzoska (1978), in his thoughtful discussion of the nature of rivers, cites Leonardo da Vinci to emphasize that this is no new problem. Only within the last two decades have we begun to see the development of such ideas as the River Continuum Concept which allow the development of theories that can be tested in a scientific manner, as is suggested by Ward and Stanford (1984) among others. Such ideas are easy to criticize, and there is a tendency to do that in an unconstructive manner; but any idea that generates testable hypotheses is valuable because that is the way that science is supposed to work. In that respect, much of ecology has moved only recently into the scientific era.

The fact remains, though, that our understanding of large rivers is based very largely on extrapolation, on somewhat shaky grounds, of what we have learned in our rubber boots and little portable boats from small rivers and streams. Considerable ingenuity has been exercised in trying to evade these limitations, and to find out directly about the biota in big watercourses. We have, of course, the somewhat dubious data on fishery yields; but they represent only the top of the ecological pyramid, and can rarely be expected to offer explanations as to why changes have occurred. Drift has been studied by various workers; there is nearly always a bridge somewhere that will serve as a platform. For example, Matter and Hopwood (1980) and Wefring and Hopwood (1981) are two of the more recent papers on drift in large water courses. It turns out that drift is often different at different depths; which is not surprising, but it does make the investigation more complex. Artificial substrates have often been used to examine the benthos. They also can be put into the water from accessible structures. Some recent papers on this technique are those of McConville (1975), Fredeen and Spurr (1978), Page and Neitzel (1979), Deutsch (1980) and Wefring and Teed (1980); and similar methods have been used on the periphyton (Waite 1979). However, as is well known from small-stream studies, artificial substrate are always selective, so while they give good comparative data, they do not tell one what is actually there on the river bed. Quite elaborate samplers have been devised, such as the airlift described by Herrig (1975), a concept that other people have also tried. But it remains difficult to select a sampler for use in deep rivers, as is discussed at length by Elliott et al. (1980).

Another approach has been to collect emerged insects, as by light-trapping Trichoptera adults (Malicky 1981; Chantaromongkol 1983), or event to collect the drifting exuviae of emerged Chironomidae with a drift net (Wilson and Wilson 1984). These are all good ideas, but at best, they can supply only a partial picture of the biota and its interactions. We need to be able to relate our findings to actual conditions within the complex of the whole environment before they become really relevant to our understanding of what is going on in the river itself. One may ask, for example, how far a pupal exuvium can drift and how far a caddisfly will fly to a light.

The problem is that we know that large rivers encompass a great variety of habitats. This was appreciated by Behning (1928) during his very early study of the Volga, and has been borne out by many studies since. I cite Barton and Lock (1979), Haynes and Markarewicz (1982), Beckett et al. (1983), and Vincent (1981) as recent examples. Important also is the fact that these different habitats have very different biological importances. Benke et al. (1985) have recently shown that what they call the snag habitat — fallen trees, piles of vegetation against impediments to flow, etc. — are very important to production, a point that has also been made by (Sedell et al. 1989) who referred to them, very aptly, as "hot spots". These places are very difficult to sample quantitatively by any available technique, and they are among the many features of large rivers that are most often removed for navigational purposes (Sedell and Froggatt 1984; Triska 1984). They may also be important organizational points in the recovery of rivers from ecological insults (Regier et al. 1989); they are perhaps important features of the well known resilience of running water biotic communities. Perhaps also the same applies to the floodplains, which shelter a host of different habitats and are a source of organic matter to the system. These have been studied very little to date, and many human activities tend to isolate them from the river and change them enormously.

Clearly, to manage the biota of large rivers in any intelligent manner, we need to know what occurs in each type of habitat and how important each habitat is to the general productivity of the whole system. We also need to know how the various species that are of particular interest to us, mainly fishes, use the various habitats.

Are young stages very dependent upon snags, do fishes feed on the sessile biota, such as Hydropsychidae, in such places, what amount of time is needed for floodplain species to spawn on flooded land, how far must certain species migrate before they are able to spawn? It is easy to frame these questions, and many others to which the manager needs the answers, even without considering such worries as cumulative toxicity, which is one of our major problems in this drainage basin where we are meeting. It is very apparent in the Great Lakes, and it may be that it is a potential hazard in all large watercourses.

But to answer all these questions, we need much more research, and that research can be done only with the proper facilities. Rubber boots and little boats are not enough. We have to follow the marine people and the Great Lakes researchers into the acquisition of better apparatus to be operated from floating platforms that are adapted to riverine work. From such platforms, we could exploit such techniques as diving that have already been explored by such workers as Rabeni and Gibbs (1978), or the even more elaborate diving shaft used by Sopp (1983) and Schmitz (1986) on the Rhine. (They call it a pit in their English summary, but that is a poor translation.) Such methods would allow on the spot study of conditions on the river bed, in snag habitats and among the various other very localized conditions that are suspected of being of particular importance to riverine biota.

When I have said this to other people concerned with rivers, their immediate reaction has been that the costs would be too great, as the vessels required would need to be custom-designed for use in swiftly flowing shallow water. It has been my thought that perhaps retired tugboats would be the ideal solution. I am sure that there is not a large secondhand market in such vessels, so they should sell for scrap prices. Their only disadvantage would be that they would cost a lot to run because of their engines. But does one need to move them around on the main power? Could they not be used like a four-wheel-drive truck and put onto the main engine only when necessary to hold station for the purpose of sampling? Anyway, cost has not prevented the oceanographers and the Great Lakes scientists from acquiring the necessary vessels to do their work, and I believe that that is because everyone realizes that such vessels are necessary. It is not quite so obvious that this is also true of large river work. In any event, it is clear that work on large rivers must continue to be enormously costly, so one of the necessary outcomes of the sort of work that I have described will be to devise some fairly simple methods for monitoring the health of the rivers. If we really understood the system, I believe that it would be possible to devise methods, such as monitoring drift or using artificial substrate, to keep a check on the general condition of the watercourse. Such simple techniques could be used for administering regulations, and to serve as warning systems that might lead to the recall of the research team in their old tugboat.

Finally, when it comes to management, we must recognize that fisheries are only one of many other interests that impinge upon rivers. These include irrigation, navigation, water supply, power generation, flood control and many other things. All these activities have effects upon the biota and have generally negative effects upon conservation. Fundamental decisions as to how to proceed, even with the best information that can be obtained, must inevitably be based upon economic and political considerations, and both are difficult and are not aided by extreme positions. I, for example, could make a good case for doing away with agriculture altogether in sensitive drainage basins, but that would clearly be ridiculous. This all goes far beyond science.

References

Barton, D. R., and M. A. Lock. 1979. Numerical abundance and biomass of bacteria, algae and macrobenthos of a large northern river, the Athabasca. Int. Rev. gesamten Hydrobiol. Hydrogr. 65: 345–359.

Beckett, D. C., C. R. Bingham, and L. G. Sanders. 1983. Benthic macroinvertebrates of selected habitats of the Lower Mississippi River. J. Freshwat. Ecol. 22: 247–261.

Behning, A. 1928. Das Leben der Wolga, zugleich eine Einfuhrung in die Flussbiologie. Die Binnengewässer, Stuttgart 5: 162 p.

Benke, A. C., R. L. Henry, D. M. Gillespie, and R. J. Hunter. 1985. Importance of snag habitat for animal production in southeastern streams. Fisheries 10: 8–13.

Boyle, R. H. 1979. The Hudson River. Norton, New York, NY. 325 p.

Carlson, C. A., and R. Muth. 1989. The Colorado River: lifeline of the American southwest, p. 220–239. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Chantaramongkol, P. 1983. Light-trapped caddisflies (Trichoptera) as water quality indicators in large rivers: results from the Danube at Verce, Hungary. Aquat. Ins. 5: 33–37.

Davies, B. R., and K. F. Walker. 1986. The ecology of river systems. Monogr. biol. 60: 741 p.

Deutsch, W. G. 1980. Macroinvertebrate colonization of acrylic plates in a large river. Hydrobiologia 75: 65–72.

Edwards, C. J., P. J. Hudson, W. Duffy, S. J. Nepszy, C. D. McNabb, R. C. Haas, C. R. Liston, B. Manny, and W.-D. Busch. 1989. Hydrological, morphometrical, and biological review of the connecting rivers of the international Great Lakes: a review, p. 240–264. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Elliott, J. M., C. M. Drake, and P. A. Tullet. 1980. The choice of a suitable sampler for benthic macroinvertebrates in deep rivers. Pollut. Rep. Dep. Environ. 8: 36–44.

Fredeen, F. J. H. 1983. Trends in numbers of aquatic inverterates in a large Canadian river during four years of black fly larviciding with methoxychlor (Diptera: Simuliidae). Quaest. Entomol. 19: 53–92.

Fredeen, F. J. H. and D. T. Spurr. 1978. Collecting semi-quantitative samples of blackfly larvae (Diptera Simuliidae) and other aquatic insects from large rivers with the aid of artificial substrates. Quaest. Entomol. 14: 411–431.

Haufe, W. O., and G. C. R. Croome [ed.]. 1980. Control of black files in the Athabasca River. Tech. Rep. Alta. Environ, Publ., Edmonton, Alta 241 p.

Haynes, J. M., and J. C. Markarewicz. 1982. Comparison of benthic communities in dredged and undredged areas of the St. Lawrence River, Cape Vincent, New York, U.S.A. Ohio J. Sci. 82: 165–170.

Herrig, H. 1975. Die Bodensauger — ein neuartiges Gerat zur Entnahme von Sohlenproben aus grossen Fliessgewässer. Deutsche Gewasserkundl. Mitt. 19: 104–107.

Lauterborn, R. 1893. Beitrage zur Rotatorienfauna des Rheins und seiner. Altwasser. Z. Jb., Abt. Syst. 7: 254–273.

1916. Die geografische und biologische Gliederung des Rheinstroms. 1. Teil. Sber. heidelb. Akad. Wiss. 7: 4: 61 p.

Liepolt, R. [ed.]. 1967. Limnologie der Donau. Schweizerbartsche Verlagsbuchhandlung, Stuttgart. 648 p.

Lillehammer, A., and S. J. Saltveit. 1984. Regulated rivers. Universitetsvorlaget AS, Oslo. 540 p.

Malicky, H. 1981. Der Indikatorwert von Kocherfliegen (Trichoptera) in grossen Fliessen. Mitt. dt. Ges. allg. angew. Ent. 3: 135–137.

Matter, W. J., and A. J. Hopwood. 1980. Vertical distribution of invertebrate drift in a large river. Limnol. Oceanogr. 25: 1117–1121.

McConville, D. R. 1975. Comparison of artificial substrates in bottom fauna studies of a large river. J. Minn. Acad. Sci. 41: 21–24.

Mordukhai-Boltovskoi, Ph. D. 1979. The River Volga and its life. Monogr. biol. 33: 473 p.

Page, T., and D. A. Neitzel. 1979. A device to hold and identify rock-filled baskets for benthic sampling in large rivers. Limnol. Oceanogr. 24: 988–990.

Rabeni, C. F., and K. E. Gibbs. 1978. Comparison of two methods used by divers for sampling benthic invertebrates in deep rivers. J. Fish. Res. Board Can. 35: 332–336.

Regier, H. A., R. L. Welcomme, R. J. Steedman, and H. F. Henderson. 1989. Rehabilitation of degraded river ecosystems, p. 86-97. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Richardson, R. E. 1921. Changes in the bottom and shore fauna of the Middle Illinois River and its connecting lakes since 1913–15 as a result of increase southwards of sewage pollution. Bull. Ill. Nat. Hist. Surv. 14: 33–75.

Roberts, J. R., and D. J. Stewart. An ecological and systematic survey of fishes in the lower Zaire or Congo River. Bull. Mus. Comp. Zool. Harv. 147: 239–316.

Rzoska, J. [ed.]. 1976. The Nile, biology of an ancient river. Monogr. biol. 29: 417 p.

1978. On the nature of rivers, with case stories of Nile, Zaire and Amazon. Junk, The Hague. 67 p.

1985. The water quality and hydrobiology of the Niger, p. 77–99. *In* A. T. Balkem [ed.] The Niger and its neighbours. Rotterdam.

Sanders, L. G., and C. R. Bingham. 1981. Two rare species of Ephemeroptera in the lower Mississippi River, U.S.A. Ent. News 92: 38 p.

Schmitz, M. 1986. Untersuchung des Makrobenthos der Stromsohle im oberen Niederrhein mit Hilfe eines Taucherschachtes. Decheniana (Bonn) 139: 363–372.

Sedell, J. R., and J. L. Froggatt. 1984. Importance of streamside forests to large rivers: the isolation of the Willamette River, Oregon, U.S.A., from its floodplain by snagging and forest removal. Verh. int. Verein. theor. angew. Limnol. 22: 1828–1834.

SEDELL, J. R., J. E. RICHEY, AND F. J. SWANSON. 1989. The river continuum concept: a basis for the expected ecosystem behavior of very large rivers? p. 49–55. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

SIOLI, H. 1984. The Amazon. Limnology and landscape ecology of a mighty river and its basin. Monogr. biol. 56: 763 p.

SOPP, E. 1983. Verteilung des Makrozoobenthos im Querprofil des Rheins bei der Loreley. Verh. Ges. Okol. (Mainz) 10: 279–285.

STALNAKER, D. B., R. T. MILHOUS, AND K. D. BOVEE. 1989. Hydrology and hydraulics applied to fishery management in large rivers, p. 13–30. *In* D.P. Dodge [ed.] Proceedings of the International River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

TRISKA, F. T. 1984. Role of wood debris in modifying channel geomorphology and riparian areas of a large lowland river under pristine conditions: a historical case study. Verh. int. Verein. theor. angew. Limnol. 22: 1876–1892.

VINCENT, B. 1981. Profondeur, vase et courant, facteurs de micro-repartition transversale du benthos dans l'estuaire d'eau douce du Saint-Laurent (Québec). Can. J. Zool. 59: 2297–2305.

WAITE, D. T. 1979. A periphyton growth substrate useful for nutrient studies in large rivers. Water Res. 13: 1347–1349.

WARD, J. V., AND J. A. STANFORD. 1979. The ecology of regulated streams. Plenum, New York, NY. 398 p.

1984. The regulated stream as a testing ground for ecological theory, p. 23–28. *In* A. Lillehammer and S. J. Saltveit [ed. Regulated rivers. Universitetsforlaget, Oslo.

1989. Riverine ecosystems: The influence of man on catchment dynamics and fish ecology, p. 56–64. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

WEFRING, D. R., AND A. J. HOPWOOD. 1981. Method for collecting invertebrate drift from the surface and bottom in large rivers. Prog. Fish Cult. 43: 108–110.

WEFRING, D. R., AND J. C. TEED. 1980. Device for collecting replicate artificial substrate samples of benthic invertebrates in large rivers. Prog. Fish Cult. 42: 26–28.

WELCOMME, R. L. 1980. Fisheries ecology of floodplain rivers. Longmans Canada, Don Mills, Ont. 317 p.

1985. River Fisheries. FAO Fish. Tech. Pap. 262: 330 p.

WHITTON, B. A. [ED.]. 1984. Ecology of European rivers. Blackwell, Oxford. 644 p.

WILSON, R.S., AND S.E. WILSON. 1984. A survey of the distribution of Chironomidae (Diptera, Insecta) of the River Rhine by sampling pupal exuviae. Hydrobiol. Bull. 18: 119–132.

ZACHARIAS, O. 1898. Das Potamoplankton. Zool. Anz. 21: 41–48.

ZWICK, P. 1980. Plecoptera (Steinfliegen). Handbuch der Zoologie. IV: 2:2/7: 115 p. Walter de Gruyter, Berlin.

A Political View of Large River Management

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Civilization began when a nameless people descended the arid Afro-Asian steppes to a fertile valley. They settled by the banks of a great river, harnessed its force, prospered and multiplied. The river was the Nile; the civilization, Egyptian. And mankind's history has been influenced by large rivers ever since.

We have used rivers for transportation and exploration, for power generation and irrigation. They supply us with drinking water, and sweep away our sewage. We credit them with a mystic ability to forge bonds between people, but we also designate them as boundaries between countries and ideologies.

We started with the Nile, and we've been tinkering with large rivers ever since. We have used and abused them. We've dredged them, dammed them, diverted them. A few — those we have no reason to exploit — are still in pristine condition. Others have been so polluted they are seemingly beyond hope. Yet their capacity to rebound from this abuse exceeds our capacity to degrade them: Witness the amazing recovery of the Thames from hundreds of years of cultural and industrial pollution.

All these roles — religious, cultural, political — mankind has arbitrarily assigned to large rivers. But how many people think of the original role assigned to them by nature — that of an ecosystem, a habitat? And how much of that fishery habitat role can fisheries managers expect to attain when there are all those other users clamoring for a share of the resource?

Do we know how to manage large rivers at all?

These are the questions you have come to this Symposium to discuss.

And I am grateful that you have come here, to Ontario, to discuss them. We need your expertise. This province is inundated with fresh water. It is no wonder that the name ''Ontario'', an Amerindian name, means ''sparkling waters''.

Our rivers run through an amazingly diverse land mass, coursing through climatic areas ranging from subarctic — complete with polar bears and seals — through to those that lie on the same latitude as northern California.

Fishing demands placed on the resource are as diverse as their terrain, from subsistence fishing by people in remote areas through to large commercial operations; our recreational fishing draws anglers from the four corners of the world.

In countries where fish from rivers constitutes the major, or only, protein food for the population, the potential production is enormous. Yet most of the literature deals with standing waters only. How do we approach this whole new field of fisheries management?

As a layman, I may not understand the more technical aspects of this gathering. But I do understand that you must contend with pollution and water quality, habitat protection and rehabilitation, the question of jurisdiction, and conflicting cultural values, and the struggle to produce a sustainable yield of fish from large rivers.

Those issues are ones that I, as a policymaker, must also deal with. I'd like to touch on a few that affect your work at a time when society is only dimly aware of the value of our large rivers. Not the least of those issues is the competition for the resource. That's something I, as a Minister of Natural Resources, can certainly understand. Competing — often conflicting — demands on renewable resources are questions I come up against every day. In fact, I can see those questions with particular clarity where large rivers are concerned. I am also Minister of Energy for Ontario, and thus greatly involved in decisions affecting the supply of hydro-electricity to this province.

But sometimes the question of competing demand is even more to the point. And I imagine that one of the most vexing questions for fisheries managers is: For which type of fishing do you plan? That which is done for subsistence, that which is done for sale, or that which is done for sport? Which takes precedence?

Here in Ontario, we live in one of the few places in the world where people are afforted the luxury of fishing simply as recreation. Our sport fishermen go so far as to participate in catch-and-release programs in which only trophy-sized fish are taken.

We find it difficult to comprehend that in other jurisdictions the health of the resource is literally a matter of life and death.

Yet we too must deal with competition for the resource, and the competition is fierce and complex. Habitat must compete with power generation — must compete with irrigation — and so on.

The current social mindset is such that we think of these uses as being mutually exclusive. But they need not be. We can compromise. For example, my ministry joined forces last year with a local municipality and three American power companies, to work on a project on the St. Marys River, a boundary water between Canada and the United States. Our project not only restored fish habitat for an historically productive fishery, it also increased power generation.

That one project flies in the face of the simple, accepted convention of applying only ''either/or'' choices in resource management. The principle of rational allocation of resources is a very new concept. Society likes to believe natural resources are bestowed upon us by virtue of divine providence; therefore, they are no one's responsibility.

That attitude has to change, and that is already happening. People are starting to realize how much we need our large rivers. Civilization was built on them, and now civilization is destroying them. Only a few years ago, we thought that just a few little chemicals dumped in our great big lakes and rivers could cause no harm. You might remember the motto: ''Dilution was the solution to pollution''. We can't justify that argument anymore.

Back in 1978, the American Chemical Society registered more than 4-million substances, and estimated the numbers were increasing by 6 000 per week.

And the U.S. Environmental Protection Agency calculated at the time that up to 50 000 chemicals could be in daily use, and that total didn't include pesticides, pharmaceuticals, or food additives.

A rough guess was that there were as many as 63 000 chemicals in common use.

A lot of these chemicals end up in our rivers, our lakes and our oceans. Here in southern Ontario, we have to cope with acid rain, a so-called dioxin ''blob'' which has settled on the bed of the St. Clair River, and the heavy pollution that is part and parcel of living in a concentrated industrial area.

Not all this pollution is our fault, and we cannot hope to combat it in isolation. For example, much of our acid rain is fallout from industries that are not even located within our borders.

That raises another question which you, as fisheries managers, must also come to grips with: the question of jurisdiction. Watersheds have no political affiliations. Many large rivers flow through more than one country: The Rhine flows through five. The Mississippi drains 31 of the U.S. states. Argentina uses three rivers as international boundaries. So who takes responsibility for what?

There is hope that jurisdictions will allow the management of large rivers to cross political boundaries. In fact, there have been some encouraging alliances.

Here in Ontario, flood control programs are managed by conservation authorities (CAs) who jointly administer flooding and erosion control programs throughout this province. CAs are organized by local municipalities, not along jurisdictional boundaries, but on the basis of watersheds. This sensible approach was revolutionary when it was devised 40 years ago; and the accomplishments by CAs in four decades have been stunning. While I cannot say Ontario's flooding problems are a thing of the past, I can say we now very rarely experience nightmarish scenes of property destroyed and lives lost. Those scenes are an annual event in some countries.

Here, where the Great Lakes are used for so many purposes, and are boundary waters as well, there are also encouraging signs of co-operation.

In 1964, water quality was the subject of an investigation by the Canadian-American International Joint Commission involving Great Lakes pollution. The result was the Great Lakes Water Quality Agreement of 1972, an agreement expanded in 1978 and again in 1983.

Water quantity was the subject of a conference held in Ontario in 1984 to discuss international co-operation in the sharing of Great Lakes water.

The following year, the ten jurisdictions which share the Great Lakes signed a charter of principles. That charter protects the Lakes from large-scale water diversions and general overuse.

What about international co-operation in the management of large rivers? There are some examples. One is the Columbia River Treaty between Canada and the United States, a means for joint development of the river basin for power generation. Its counterpart in Asia is the Indus Water Treaty of 1960, an agreement which ended 13 years of negotiation between Indian and Pakistan over rights to those waters. With signposts like these, there is hope for international fisheries management agreements involving large rivers.

Another facet of the jurisdiction question involves regulatory functions. In an ideal situation, one would expect resources to be managed in an holistic way. In reality, as you no doubt already have found, you have to deal with a maze of authorities to achieve your objectives — at municipal, state and federal levels, as well as internationally.

Here in Ontario, for example, responsibility for fish and wildlife is vested in my ministry, the Ministry of Natural Resources. Power generation is largely the responsibility of Ontario Hydro. The Ministry of the Environment has the mandate for pollution control. And on it goes.

The question of jurisdiction — particularly over international waters — leads us to another issue. Not only must one contend with reconciling conflict between jurisdictions but also with a clash of values and cultural attachments when a resource is shared.

To which ends do you apply your efforts? For which species do you maximize production — do you encourage the species with sport qualities? the species yielding the greatest source of protein? the most marketable species? all of the above? Yours is an unenviable task.

None of the considerations I have outlined are wholly based in science. They are, rather, practical observations that I as a layman can see coloring your perceptions and conclusions about river and fisheries management.

Your work is science. That science is shaped not only by nature, but by culture, politics, economics, and the attitudes of society.

I believe the biggest hurdle to be faced in managing large rivers as fisheries is in changing people's attitudes to the resource — to the habitat in which fish live, and to the product itself.

I use the word ''product'' advisedly. Make no mistake about it — countries will manage fisheries only if the national economy can be improved by such management.

Whether it's dollars or drachmas — whether by way of tourism or fleets of trawlers — people understand that fishing means money. Yet they don't understand it also means making a calculated investment in the resource. The underlying attitude is that fisheries are God-given and nature-driven. People will argue that we don't need to actively *do* anything to preserve and develop the resource. They must be shaken out of that complacency. The work you are doing here is a start.

The fisheries of the future could well be our large rivers. The beginning of that future could well be here and now. This is your moment. I have no doubt your work will be the fountainhead of the new literature about our most ancient — and our most underestimated — resource.

Hydrology and Hydraulics Applied to Fishery Management in Large Rivers

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Abstract

STALNAKER, C. B., R. T. MILHOUS, AND K. D. BOVEE. 1989. Hydrology and hydraulics applied to fishery management in large rivers, p. 13–30. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The use of engineering models from hydrology, hydraulics and sedimentation studies for describing physical habitat conditions for fishes in large rivers is reviewed. Examples of specific mathematical and computer models are presented and recommendations for application to spawning, incubation and microhabitat evaluations are made.

Résumé

STALNAKER, C. B., R. T. MILHOUS, AND K. D. BOVEE. 1989. Hydrology and hydraulics applied to fishery management in large rivers, p. 13–30. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Les auteurs examinent l'utilisation de modèles technologiques tirés d'études hydrologiques, hydrauliques et sédimentologiques pour décrire les conditions physiques des habitats des poissons dans de grands cours d'eau. Des exemples de modèles mathématiques et informatisés sont présentés et des recommandations concernant leur application à l'évaluation de frayères, de zones d'incubation et de microhabitats sont suggérées.

Introduction

Fishes and other aquatic organisms that live in rivers are subjected to a much different type of environment than are organisms that live in standing water. Two characteristics of rivers distinguish them from virtually all other types of aquatic environments: wide variability, in both time and space, and the presence of a continuous current. Currents that may occur in other aquatic habitats are usually not as pervasive, spatially and temporally varied, or as strong as they are in rivers.

River dwelling organisms are well adapted to this specialized environment. Some adaptations are morphological, such as the streamlining and flattening of body shapes and others are behavioral, such as the use of low velocity areas adjacent to high velocity areas. Use of these ''micro components'' of the habitat allows a high delivery of food with little energy expenditure, thus optimizing the individual's energy budget. Other species are better adapted to lentic environments, and select riverine habitats that are as much like a pond as possible. The common attribute of all these adaptations is that the areas inhabited by a species tend to favor its growth, survival, and reproduction, and often isolate the species from competitors and predators (Hynes 1970). Furthermore, the use of microhabitats changes as the organisms grow, and with changes in diel activity and season (Everest and Chapman 1972). Thus, a species may require many specialized microhabitats during the course of its life history.

The formation of these microhabitat areas is the result of a complex interaction between the morphology of the stream channel and the flowing water. Channel morphology plays a major role in determining the distribution of depths and velocities at a particular discharge, but is itself a result of the overall stream hydrology and the materials through which the stream flows. The streamflow can change very quickly, whereas alterations in physical morphology usually occur over an extended period. The use of mathematical and computer models, adapted from engineering hydraulics, are reviewed in this paper with recommendations given for application to fishery management in large rivers.

Fishery and water resources managers must collectively understand the consequences of various river control and management schemes. A common language needs to be established for evaluating the fishery on an equal basis with the other uses of river water. Such an understanding was emphasized by Winger (1980) in his review of the physical and chemical characteristics of warmwater streams. ''Management and protection of warmwater stream resources depend on a thorough understanding and comprehension of the interrelatedness of streams and their valleys. Tantamount to that understanding is the effective conveyance of that information to decision and policy makers. Consequently, fishery managers and biologists should acquire a working knowledge of the fluvial dynamics, hydrologic processes, and geochemical relationships that control these systems.''

Over the last two decades, engineering technology has provided tools for describing and predicting the physical processes occurring within a stream. To a lesser extent, channel dynamics can also be analyzed by using historical studies and simulation modeling. Fish habitat models based on physical and chemical variables have been developed to describe and simulate the dynamics of the riverine habitat over time and space. The physical processes of hydrology, hydraulics, and sedimentation, and their integration, provide the theoretical basis for understanding the habitat consequences of river manipulations and management and can be used to formulate hypotheses of biological responses that should be the focus of future research (Trihey and Stalnaker 1985).

The primary purpose of habitat simulation is to describe the relationships between the streamflow and the usable quantities of the physical habitat in the stream. The function of physical habitat versus streamflow can be used not only to simulate habitat conditions over time but also as a surrogate for an economic production function in water management decisions. The physical habitat represents the space in a river that can be used by a specific species and life stage of fish. The assumptions and calculation procedures used to determine one form of a physical microhabitat vs. flow function were described by Stalnaker (1979). The river surface area usable for certain recreational activities can also be simulated as a function of streamflow (Scott and Hyra 1977[1]; Fritschen et al. 1984).

Definitions

Large vs. Small Rivers

Stream classification has been a subject of several publications where particular interest was focused on fluvial processes and sedimentation in river geomorphology (Leopold et al. 1964; Morisawa 1968; Dunne and Leopold 1978). This literature illustrates that the characterization of rivers as large or small is very arbitrary, since the geometry and hydraulic aspects of streams are often similar in small wadable streams and large deep rivers.

We make no distinction here between large and small rivers insofar as the physical processes are concerned. Large rivers may have beds of gravel or sand; they may be cold or warm; and the gradient may be high or low. From a fishery biologist's viewpoint, large rivers are a matter of scale — and scale becomes important when one describes and measures important habitat variables. In practical terms, we consider any stream large if it has an average depth over 1 m and requires measurements to be taken from a boat with specialized gear. Another generality related to working on rivers is that the larger the river, the more specialized the gear requirements.

Although there are many similarities between habitat simulations in all rivers, several characteristics of large rivers require different procedures from those used in small rivers: the vertical velocity distribution is usually more important in large rivers; much of the information on habitat tolerances and preferences of species are derived from small rivers, and may require transformation or extension before they are applicable to large ones; organisms in large rivers often show a greater tendency toward habitat zonation and isolation and the use of specialized habitat types; and the emphasis on specialized habitats by these species may require more of a two-dimensional analysis of temperature and water quality than is typically needed in small streams.

Gravel vs. Sand-Bed Rivers

The principal difference between a gravel-bed river and a sand-bed river is the size of the bed material and the movement of sediment in the bed. In a sand-bed river, the bed is moving continually except during a few low flow periods. In contrast, a gravel-bed river is stable except during relatively high flows. Critical discharge levels capable of bed movement are consequently related to the size of the gravel in the stream.

The ecological consideration of fines (particles < 1 mm diameter) differs between gravel and sand-bed rivers. In a sand-bed river the fines are continually cycled as deposits into the bed and then resuspended. In a gravel-bed river, the fines are absorbed into the bed gravels when the flow is low and are flushed from the gravel when flows exceed a certain discharge. This "flushing flow" is related to the size of the particles on the bed surface.

Habitat Models

The many stream habitat models developed during the past 30 years have been primarily responsive to particular threats to the stream fishery. In general, the models fall into one of four categories: physical microhabitat; water quality; cover and channel structure; and the general "health" of the stream substrate. These models focus on a few variables that are assumed to be important to the success of riverine fish and invertebrate species and that are used to assess specific potentially detrimental activities: streamflow alteration; pollution; channelization and realignment; and timbering, grazing, farming, and other sediment producing land-uses. The variables chosen for each class of models have been selected primarily because they are known to be significantly altered by the development activity and also are important from a biological perspective. The biological importance is usually supported by basic research of species responses to changes of the variables as reflected by changes in behavior, mortality, growth, reproductive success, or year-class strength.

Important research continues to contribute to the habitat concepts of stream ecology in the form of multiple regression analyses, in which fish standing crop is the principal dependent variable. Such regression models (Binns and Eiserman 1979) show that certain stream habitat variables are consistently important determinants of the condition or success of fish populations. These habitat models were recently reviewed by Fausch et al. (1988).

Microhabitat, macrohabitat, and habitat — terms commonly seen in literature on fluvial environments — are often used interchangeably. Gosse (1982)[2] defined microhabitat

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[1] Scott, J. W., and R. Hyra. 1977. Methods for determining instream flow requirements for selected recreational activities in small and medium size streams. Paper presented to the 13th annual water resources association conference in Tucson, AZ. Available from Aquatic Systems Branch, National Ecology Center, 2627 Redwing Road, Fort Collins, CO 80526-2899, USA.

[2] Gosse, J. C. 1982. Microhabitat of rainbow and cutthroat trout in the Green River below Flaming Gorge Dam, Vol. I. Utah Division of Wildlife Resources. Contract #8/5049. 103 p. Available from Aqua-Tech Biological Consulting Firm, Logan, Utah 845321, USA.

as "those physical . . . variables which define the precise location occupied by a fish, and which would or could change with small changes in fish's location." Microhabitat variables "refer to those physical variables which appear to be used by the fish to select their location." Microhabitat has both structural and hydraulic characteristics. Several variables are common to most microhabitat models: water velocity; fish (nose) velocity; water depth; fish depth; substrate particle size, degree of embeddedness, and percent fines; overhead cover (e.g., undercut banks, root wads, overhanging vegetation); and instream cover (e.g., velocity shelter downstream of submerged objects, depth, surface turbulence).

Bovee (1982), in discussing the change in species composition in a stream from headwaters to the mouth, noted that "numerous authors have reported the addition or replacement of species as a function of stream order, stream size, gradient, or other descriptions of longitudinal gradations of environmental conditions ... the 'longitudinal succession' of species as a function of variables such as mean depth, mean velocity, temperature, water quality, or other characteristics exhibiting gradational change. This perspective might logically be defined as a macrohabitat approach to riverine ecology."

Hydraulics

The purpose of hydraulic simulation is to describe the velocity distribution and water surface elevation for specified discharges in a river. The assumption is made that fishery and water resources can be better managed if the two are linked by common physical characteristics that are a function of streamflow alterations. The important physical habitat variables that result from hydraulic simulations are the velocities, depth, wetted perimeter, channel width and surface area. The interaction between these hydraulic variables and the structural features of the channel determine the dynamics of the microhabitat over time and space.

Hydrology

Hydrology is defined as "the applied science concerned with the waters of the earth in all its states — their occurrences, distribution, and circulation..." (American Society of Civil Engineers 1962). In the present work, the term is restricted to concerns related to the processes in rivers. The two processes of most concern are the variations in streamflows and sedimentation. For convenience, we discuss sedimentation as a separate process. When we use the term hydrology, we refer to the time pattern of streamflows. These streamflows may be instantaneous, daily, monthly, annual average or annual peak flows. Although we do not discuss them in detail, hydrologic changes can have a significant impact on the fluvial process within the stream.

Sedimentation

In North American terminology, sedimentation tends to include the process of erosion, transport, and deposition of sediment. The use of the term, however, is not clear and unambiguous. In this paper, we refer to the movement and characteristics of the sediment within the stream channel, and the processes that may change the channel characteristics, including cross-sectional morphology.

The characteristics of the aquatic community within a stream are strongly related to the yield of both sediment and water from a watershed (Fig. 1) (Cairns 1968; Reiser et al. 1985). The effects is a product of both the geology and climate of the area. For example, the aquatic community of a stream in an arid region of granitic materials is far different from that of a stream in a humid region with bedrock ledges. The stream channel can change as a result of naturally occurring flows and sediment yield and as a result of changes in the amount and pattern of flows induced by man.

Concepts of Riverine Habitat Analysis

Habitat Models

All flow/habitat models have two common elements: a procedure for describing changes in model variables as a function of discharge; and a transformation of raw values for these variables (e.g., a dissolved oxygen [DO] concentration of 4 mg•L^{-1}) into biological terms (e.g., trout die if the DO concentration falls below 4 mg•L^{-1}).

Nearly all riverine habitat models that do not distinguish between micro and macro features contain variables that describe the average physical environment. These include variables such as wetted surface area, wetted perimeter, mean depth, mean velocity, average condition or percent area with specified substrate and cover, and mean, maximum or minimum temperature. A subset of these models includes terms that describe the average chemical environment, incorporating variables such as DO, alkalinity, nitrogen compounds, phosphate, pH, or other chemical

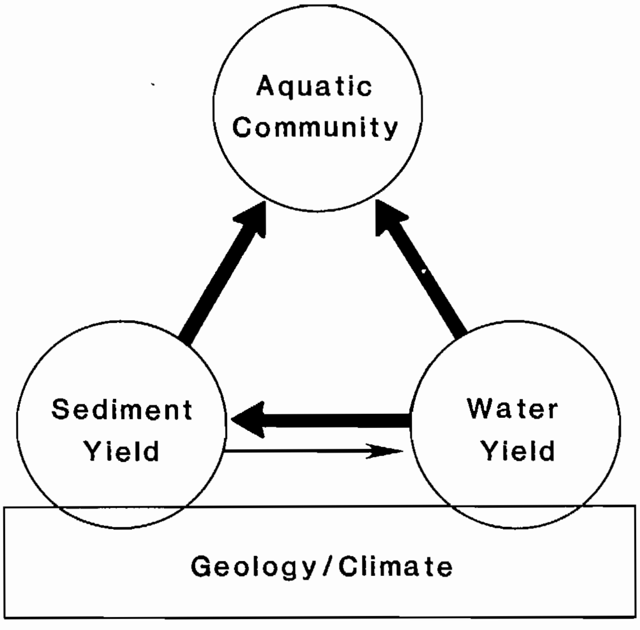

FIG. 1. The aquatic community as an end product of water and sediment yield from the watershed.

constituents, all averaged over the stream cross section for a specified time period. In a few models, attempts have been made to include certain aspects of the biological environment, with variables such as food supply, competitive species, and predators.

Most riverine habitat models are one-dimensional; the value assigned to a variable represents the average condition for a single cross section, or sometimes for a short reach of stream (<5–7 times channel width). Examples of commonly used one-dimensional models are the Wetted Perimeter Model (Nelson 1984)[3], the Instream Temperature Model (Theurer et al., 1982), the Habitat Quality Index (Binns and Eiserman, 1979), and the Habitat Evaluation Procedures (USFWS 1980). A few are two-dimensional, where both the longitudinal and lateral distributions of variables are measured and analyzed. Two examples of two-dimensional physical microhabitat models are the Washington method (Collings 1972) and the Physical Habitat Simulation System (Stalnaker 1979; Milhous 1979). At least one habitat modeling system--the Instream Flow Incremental Methodology (IFIM) described by Bovee (1982) — combines the use of one-dimensional and two-dimensional models. No three dimensional habitat models are now in use, although PHABSIM can potentially be modified to incorporate three dimensions. Physical process models in three dimensions that provide input to three-dimensional microhabitat models are not yet operational. The multitude of riverine habitat models were discussed by Wesche and Rechard (1980), Loar and Sale (1981), and Morhardt (1986).

A further distinction among riverine habitat models can be made by considering whether they are empirical or based on physical processes. The investigator who uses an empirical model typically must remeasure the model variables to quantify the habitat whenever the river flow changes. A physical process model is useful for predicting (simulating) changes in the environment under conditions that were not (or could not be) measured. Most often, these simulations are restricted to unmeasured discharges and hydrologic events, but can also demonstrate changes in channel morphology, waste water treatment, or the discharge of altered thermal effluents (among a myriad of possibilities).

An advantage of the empirical approach is that the investigator does not need to understand why a variable changes, but merely know how to measure it when it does change. It is also possible to include many variables in an empirical model, since functional linkages among them are not necessary. Most empirical models for river management simulations have three primary disadvantages:

1) They are data intensive, requiring the remeasurement of all variables whenever conditions change.
2) The total range of conditions for each variable is difficult to describe empirically and thus resists generalization. Consequently, any variables included in the model that are untested over a range of conditions tend to reduce transferability and the model represents only the conditions that prevailed at a specific time and place.
3) Perhaps most important, empirical models are constrained in their capabilities to quantify habitat conditions resulting from unique combinations of variables that were not measured. This third problem is illustrated by the inability of a purely empirical model to estimate the impact of a new water development project until after the project has been built and operated. Such a constraint severely limits the utility of the model for planning, and usually leads to a request for severe "constraints" being placed on the operational flexibility of new projects. This can also lead to conflicts between instream uses of water and the development of water.

The use of physical and chemical processes to derive models for habitat analyses overcomes many of the disadvantages of empirical models, although the different models vary widely in accuracy and precision. These models generally require fewer data, are capable of more generalization, and (when used properly) enable predictions of changes in the habitat under conditions when no measurements were made. The most serious drawback is their being based on mathematics, and thus requiring that the user have substantial skill and understanding. Use of these models often requires considerable judgment regarding the reliability of the results, based on knowledge of model limitations, performance, and calibration accuracy — in contrast to empirical models, which are rather straightforward but require multiple data sets.

Hydraulic Models

Many aspects of the hydraulic component of habitat analyses in rivers are similar, regardless of the size of the stream. However, the procedures for measurement and prediction of certain variables differ and some of these differences are size related. The primary hydraulic variables of concern are the water surface elevation (stage), and the distribution of velocities.

Water Surface Elevations (Stage) — To determine the depth distribution in a stream, one needs two types of information: the cross sectional bed elevations and the water surface elevation. The depth at any point on the cross section can be calculated merely by finding the difference between the bed elevation and the water surface. Bed elevations can be determined by surveying or sounding techniques. Because water surface elevations change whenever the flow changes, determinations of the water surface elevations at unmeasured discharges are a necessity.

Three methods are routinely used to determine the relation between water surface elevation and discharge: (1) Step-backwater models, which incorporate the Manning equation and energy balancing concepts (Chow 1959); (2) Models that use the Manning equation at a cross section (Chow 1959; King and Brater 1963; Morisawa 1968); and (3) Regression models that relate water surface elevation to discharge (Leopold et al. 1964; Carter and Davidian 1968).

Each of these approaches has its strengths and limitations, and its applicability is a function of the stream characteristics. The step-backwater model is most applicable in low gradient rivers with uniform to gradually varied flow, and

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[3] Nelson, F. A. 1984. Guidelines for using the wetted perimeter (WETP) computer program of the Montana Department of Fish, Wildlife, and Parks. Bozeman, MT. 25 p. + appendices. Available from Montana Fish and Game Department, Helena, MT, USA.

large upstream backwaters. The use of Manning's equation is more appropriate in steep streams with short backwater effects. The stage-discharge (regression) approach may be used in all types of rivers, provided that the cross section is not subject to a variable backwater. Large rivers may be steep and vary rapidly, but most are low gradient and vary gradually; therefore the step-backwater model is the most commonly used approach to predict water surface elevations in large rivers. Table 1 lists several computer programs that are available to predict the water surface elevation at unmeasured streamflows.

TABLE 1. Computer programs for determining water surface elevations.

Name	Type	Source
IFG4	Regression	U.S. Fish and Wildlife Service
MANSQ	Manning	U.S. Fish and Wildlife Service
R2-CROSS	Manning	U.S. Forest Service
PSEUDO	Step-backwater	U.S. Bureau of Reclamation
WSP[a]	Step-backwater	U.S. Fish and Wildlife Service
WSP2	Step-backwater	U.S. Soil Conservation Service
HEC-2	Step-backwater	U.S. Army Corps of Engineers
HEC-6	Step-backwater	U.S. Army Corps of Engineers

[a]Modified and expanded from the PSEUDO program of the U.S. Bureau of Reclamation.

Velocity — Another common attribute of habitat studies is the prediction of the velocity distribution at different water discharges. This feature distinguishes two-dimensional microhabitat analysis from most other types of river studies. Although it may be sufficient to determine the average cross-sectional velocity for certain types of studies, microhabitat analyses often require prediction of the lateral, longitudinal, and vertical velocity patterns in the river. There are basically two ways of making these predictions: (1) by empirical regression; and (2) by a more theoretical approach based on the concept of conveyance.

The water column velocity can be measured at the same locations in the river at three or more discharges to develop log transformed regressions between the measured point velocities and total stream discharge. The concept of conveyance uses the Manning equation to distribute velocities within the channel at different flows. Both techniques usually employ a mass balancing feature that ensures that discharges predicted by the simulation will equal the discharges originally input for stimulation. Either method can be used in the IFG4 program (Milhous et al. 1984), but the conveyance approach is preferred for two reasons: (1) it is mathematically stable when extrapolated over a wide range of flows; and (2) it often produces more accurate results with fewer data. At least three flows must be measured to develop an empirical velocity–discharge relation, whereas equivalent results can be obtained from only one flow measurement by using conveyance. The conveyance method is also superior when the current direction of the stream changes as a function of discharge (Fig. 2). In this example, the stream meanders more at low flow than at high flow, and the current streamlines change around obstacles as the discharge changes. Such streamline shifts cannot be satisfactorily simulated by using log-linear regression, and may lead to some of the mathematical instabilities of this approach. Because each flow pattern is independently calibrated under the conveyance approach, streamline shifts can be simulated, although it does require measurements of the velocity distribution at more than one flow.

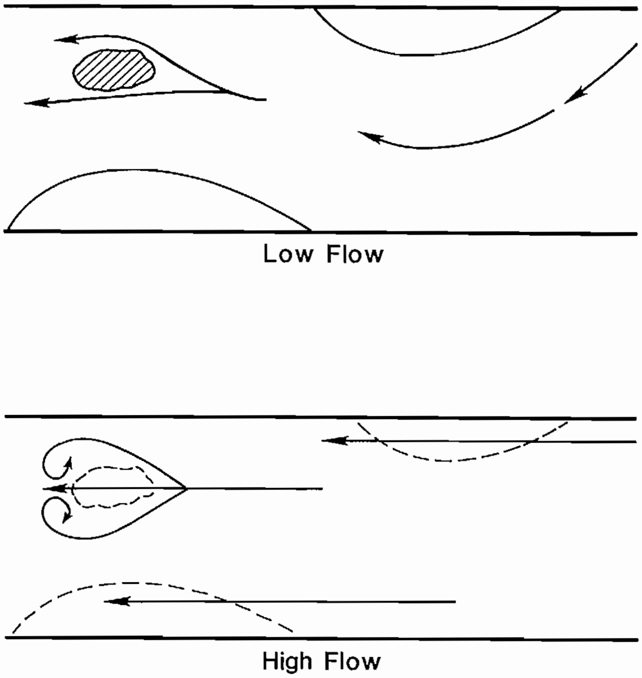

FIG. 2. Example of shifts in direction of current in a stream between low flow to high flow.

Velocity at fish location — In small rivers, the water is often so shallow that measurements of the mean column velocity closely approximate the velocities experienced by the fish, conventionally termed the "nose velocity." On the other hand, the mean column velocity in a large river may considerably exceed the near-bottom velocity faced by bottom-oriented species. The fish respond to changing discharges by changing their position in the water column — often by moving toward the bottom. Therefore, rather than the mean column velocity, the nose velocity must be used in habitat analyses in large rivers for determination of habitat suitability. If mean column velocity is used, suitability will be considerably underestimated. Annear and Condor (1984) concluded, for example, that output from the USFWS microhabitat simulation model PHABSIM was biased toward low discharges when it was applied in large rivers. This conclusion may have been the result of using mean column velocity rather than nose velocity in the habitat computations.

In conducting analyses involving nose velocities it is necessary to transform the mean column velocities from the hydraulic simulation model to the nose velocities used in the habit analysis. This transformation can be made empirically or from a theoretical distribution. To convert mean column velocities empirically, one must measure *both* the mean column and nose depth velocities during the collection of calibration data. These measurements are then used to calibrate an empirical regression equation. One form of this equation follows.

(1) $V_{(n)} = V\,[a(Y/D)^{b}]$

where $V_{(n)}$ = the nose velocity, V = the mean column velocity, Y = the nose depth, D = water column depth, a = regression intercept, and b = regression slope.

Two theoretical approaches can also be sued to translate the mean column velocity to another point in the vertical. The first is the one-seventh power law (Schlichting 1968), which is similar in form to equation (1), except that the coefficient (a) is set to a value of 1.15 and coefficient (b) to 0.143:

(2) $Vn = V\,[1.15(Y/D)^{0.143}]$

Another approach is to use a form of the Prandtl–von Karman equation:

(3) $$V_{(n)} = \frac{\log 33.35\ (Y/D_{65})}{\log 12.27\ (D/D_{65})}$$

where $V(n)$, V, Y, and D have the same definitions as above, and $D(65)$ is the particle size diameter that exceeds the diameter of 65% of the materials in the substrate.

Coefficients for the Prandtl–von Karman equation were derived in design channels under relatively uniform flow conditions (Chow 1959). Habitat studies are usually conducted in stream reaches having nonuniform and complex channel characteristics that may not conform to the conditions under which the theoretical relationships were developed. Generally the use of any nose velocity transformation is superior to the use of mean column velocities in large streams, but the development of site specific relation is the best overall approach. Unless further research verifies that equations (2) and (3) generally hold in large rivers, the empirical approach exemplified by equation (1) is recommended for determining nose velocities.

Specialized Microhabitats in Large Rivers

Cover — One distinction between assessments of habitat in large and small rivers is the relative importance of cover in influencing the tolerances of fish to different hydraulic conditions. At least two distinct behavior patterns appear to be associated with cover, and both have relevant implications with respect to river size. The first behavior has been described by the use of "cover-conditional criteria," which implies that the ranges of depths and velocities selected by a species are conditioned by the cover type available (Bovee 1982; 1986). This behavior shift is exemplified by the use of shallow water when overhead cover is present, but deep water when it is lacking. The prevailing theory is that, in the second instance, fish use depth as a form of overhead cover.

The second category of cover-related behavior is a true affinity by some species or life stages for certain types of cover. These species are nearly always associated with cover, but may tolerate a fairly wide range of hydraulic characteristics where their favored cover type is present. It is also conceivable that certain species exhibit a combination of both categories of cover use.

Such differential behavior can create errors in large-river analyses, because most of the available information on the microhabitat requirements of fish has originated from small streams. The proportion of the surface area affected by some form of overhead cover is much greater in a small stream than in a large one. If the species has a cover-conditional behavior pattern, the depths used in a cover-dominated stream may be much shallower than those used by the same species in streams without cover. Since most of the surface area of a large river is devoid of overhead cover, the suitability of shallow water may, therefore, be overestimated using criteria from small, cover-dominated streams.

Edge — A very different effect may occur in species that do not use depth as cover and are rarely found in the absence of structural overhead cover. In large rivers, the only area with an appreciable amount of structural overhead cover consists of a strip along both edges. What happens in the middle of the river is of little importance to the habitat needs of these species, except by its hydraulic connection with the edge. For these species, an investigator can often confine most of the detailed habitat description to the edges of the stream, and measure the center of the channel only superficially. The center cannot be ignored, however, because the water level in the main channel controls the depths and velocities along the edges.

Backwaters — Other specialized microhabitat types, characterized by low current velocities or specific substrate types, may also occur only along the margins of the stream. These areas may compose less than 10% of the surface area, but contain 90% of the fish in a large river. Examples of these specialized habitat features include side channels around islands, connected sloughs and oxbows, and the mouths of tributaries. The investigator is sometimes primarily interested in these localized areas, but more often includes them in conjunction with other habitats and an analysis of the entire channel. It is usually possible to treat these specialized habitat types as separate stream components, essentially independent of one another. This approach facilitates data collection and analysis, but requires additional data and special procedures for implementation.

Floodplains — Another type of specialized microhabitat that may be important in large rivers is the floodplain. Although it might be argued that all streams have floodplains, their size and extent appear to increase with stream size. As the discharge increases in many rivers, the available suitable habitat tends to decrease due to excessive velocity in the middle of the channel. This phenomenon is related more to the channel structure than to the size of the river, but the general trend is for the usable habitat to be compressed toward the river margins, as the discharge increases. Following this logical sequence, it is likely that the most constraining conditions will occur at or near bankfull discharge. Once the river overtops its banks, the amount of usable habitat expands rapidly as the floodplain is covered. Unfortunately, many riverine habitat studies have not included the floodplain as part of the model. Consequently, overbank flows are erroneously simulated as within-channel flows. This error creates several problems in the habitat analysis, not the least of which is the omission of the floodplain microhabitat. The relation between stage and discharge that holds for flows up to bankfull sometimes changes when the river expands onto the floodplain. Failure to adjust for this expansion results in the overestimation of depths and velocities in the main channel at overbank flow. This overestimation may artificially depress the estimate of suitable habitat at high flows. The combination of these errors may lead to an erroneous conclusion that high flows provide little or no habitat.

Another management problem associated with the omission of floodplain analyses relates to channel morphology. It is generally recognized that high flows are important for maintaining the existing channel structure and dimensions, and for cleansing the substrate by removing accumulations of fine materials. A commonly used estimator for a channel maintenance discharge is the bankfull discharge, which is taken as the maximum instantaneous flow with a recurrence interval of about 1.5 yr (USFS 1986). This flow is, by definition, the discharge that is equalled or exceeded within that recurrence period. The probability that the flow will remain exactly at bankfull for a significant period is much smaller than the 2 out of 3 yr implied by the recurrence interval. By recommending that the bankfull discharge be delivered for several days or weeks as a channel maintenance flow, the investigator may inadvertently design a water management regime that is detrimental to fish that could otherwise move onto the floodplain during high flow events. Inclusion of floodplain habitat usually reveals that flows slightly above bankfull provide high-flow refuge microhabitat.

Temperature and Water Quality

The issues of water quality and temperature are sometimes complex when one analyzes specialized habitats in large rivers. Most water quality and temperature models used in river analyses are one-dimensional; they provide an estimate of the average concentration of water chemistry constituents or the temperature for the entire cross section of the stream. Complete mixing is assumed and the output variable is assumed to have the same value at all locations across the cross section. Habitat models incorporating temperature and water quality variables based on one-dimensional descriptions are therefore usually considered as "macro" models. Threshold criteria based upon mean daily water temperature are typically used in conjunction with such macro models (Brungs and Jones 1977; Coutant 1977).

A typical output from such models is a longitudinal profile showing temperature along a specified length of watercourse. As illustrated in Fig. 3, it is possible to obtain families of longitudinal profiles representing different hydrological, meteorological, thermal loading, or chemical loading conditions.

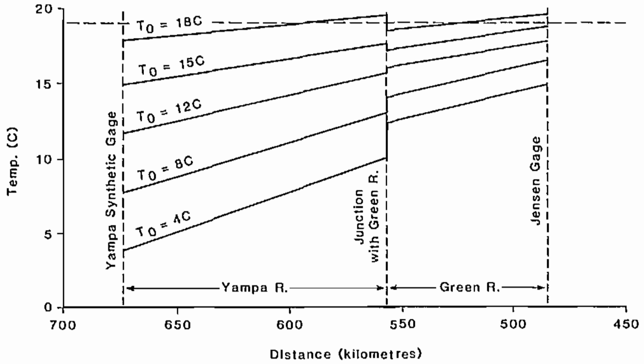

FIG. 3. Longitudinal temperature profiles from the Yampa and Green Rivers for normal July hydrometeorological conditions (Theurer et al. 1982).

The use of one-dimensional water quality and temperature models may be appropriate in most situations. However, there may be occasions when it would be desirable to be able to predict these characteristics in a more nearly two-dimensional fashion. For example, the average water temperature may be several degrees higher in backwater areas than in the main channel. This difference may have important implications about the growth of young fish. The mouths of tributaries may serve as local refuges during episodes of low DO in the larger river, where prediction of the average main channel condition is not entirely adequate.

In addition, low gradient rivers with long deep pools interspersed with shallow riffles or bars may stratify thermally during low flows in summer. Cooler, denser upstream water may slide beneath the warmer pool water, forcing cool-water species (in the absence of groundwater discharge) into a narrow band along the bottom. In other situations, the inflowing water from upstream may be warmer than the pool water and consequently flow over the top of the pools. If this condition persists long enough, DO may become depleted in the pools. Two-dimensional water quality models commonly used in small reservoirs may be adequate for predicting these occurrences. Data needs for model calibration become large, and computer time for long-term simulations become prohibitive, due to the complexity of these models.

Prediction of these variables in a specialized habitat type may not require the use of a two-dimensional model, but rather a nontraditional use of one-dimensional models. Two basic approaches are suggested: in habitat types such as side channels, it may be possible to subdivide the reach and use a one-dimensional model to predict the localized average side channel condition; and in small specialized habitat types a combination of one-dimensional modeling and site specific empiricism may provide the answer.

Certain specialized habitat types, such as connected sloughs and oxbows, have relatively low water exchange rates with the main channel. The hydraulic connection with the river is usually through a small inlet, or by groundwater inflow and outflow. In either event, water may flow directly through the slough area only during floods. A simple equilibrium temperature model applied to the slough area may be completely adequate — as a one-dimensional dissolved oxygen model would be.

A similar approach could be taken to estimate the dissolved oxygen concentration in backwater areas formed at the mouths of tributaries. Here, it would be necessary to define the area of the backwater and estimate the relative contributions of the main channel and the tributary to the volume of the backwater. One-dimensional DO models could be applied to both the tributary and the main stem to predict their respective DO concentrations and a simple dilution equation used to compute the mixed DO concentration in the backwater.

Where the hydraulic connection is more direct, and the main channel is the sole water source, a combination of models may be more appropriate. An example of this type of habitat is a side channel backwater, where the temperature of the water at the inlet to the side channel is the same as that of water in the river. However, depending on the travel time through the side channel, the water at its lower end might be considerably warmer. One solution is to treat the side channel as an independent stream. By determining the inlet temperature and side channel flow from independent one-dimensional models of the main body of the river, a simple temperature model can be used to calculate temperatures in the side channel.

Some backwaters meet none of the descriptions given above, but are formed as depressions along the bank or on the lee sides of point bars in the river. In such areas, the concentrations of dissolved chemicals may be very close to those in the main channel, and a one dimensional water quality model may be totally adequate. However, if there is considerable disparity between the temperature measured in these backwaters and in the main channel, a combination of theory and empiricism may be required. The simplest conceptual approach is to develop a series of monthly or seasonal regressions between the temperature in the backwater and the average temperature of the main channel. Then, by using a physical process model on the main stream, one can predict the average temperature at the longitudinal location of the backwater. The backwater temperature can then be estimated by using the appropriate regression. Use of this approach dictates accounting for local channel features such as orientation, topographic shading (e.g., canyon walls), and vegetation that affect the amount of sunlight reaching a specific area of stream. If these variables are not accounted for, it is unlikely that a consistent relation will be found between main channel and backwater temperature. Either the data must be stratified according to similar topographic features, or they must be entered as variables in a multiple regression equation.

Simulations in Specialized Habitats

Side Channels — We illustrate the procedures used in the analysis of side channel habitats by referring to the Palisade site on the Colorado River near Grand Junction, Colorado. The river in this vicinity is typified by repetitive cycles consisting of a small rapids, a long deep pool, and an island with a divided flow section (Fig. 4). The species of interest in this section is the Colorado squawfish (*Ptychocheilus lucius*), which uses a variety of microhabitat types at various phases of its life history. Although the adults are believed to spawn over coarse substrates in fast water, they otherwise live in deep pools and eddies. Shallow backwaters are apparently necessary for rearing young squawfish (Tyus et al. 1984; USFWS 1985)[4]. All of these habitat types are present at the Palisade site, but most of the shallow backwater habitat is associated with the small side channel on the southeast side of the island (Fig. 4). The morphology of the side channel is similar to that of a small stream, with a riffle-pool sequence repeating about every 100 m. (The distance between riffles and pools in the main channel is more nearly 2 000 m.)

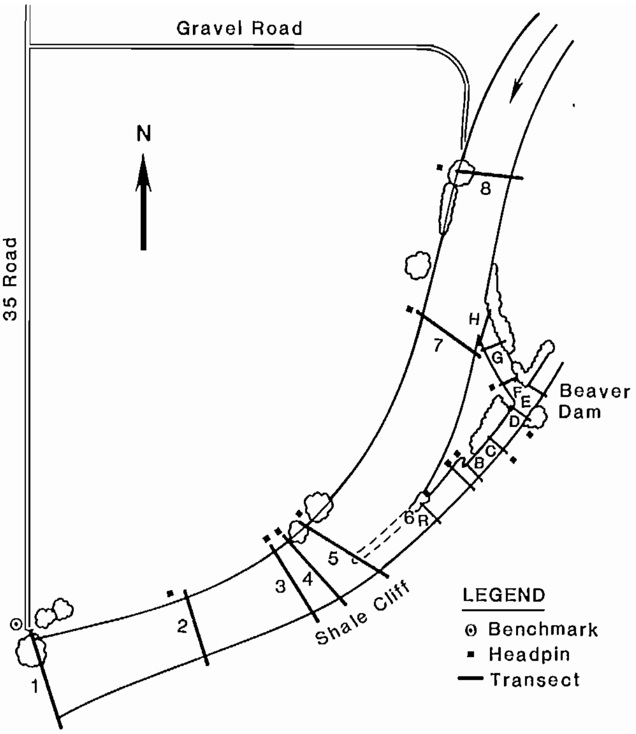

FIG. 4. A microhabitat study site on the Colorado River showing transects, benchmarks, and headpin locations.

Most hydraulic simulations must be started at a hydraulic control, a physical feature in the channel that establishes the stage-discharge relation for an upsteam section of river. However, the first side channel transect (i.e., the south end of transect 5 in Fig. 4) is a variable backwater; the stage at this location is determined by the stage at transect 4, which is ultimately controlled at transect 1. There is a clear division of flow between the north and south ends of transect 5. The water surface elevation is about 0.5 m higher on the north side than on the south side. To enable treatment of the side channel as a separate stream, the stage-discharge relationship at transect 5 was determined empirically. Once this determination was made, a starting water surface elevation was known, and the hydraulic simulation could proceed. The second relation that was needed was the amount of discharge in the side channel, during different discharges in the main channel. Transect 7 on the main channel and transect H on the side channel were placed to determine the total discharge at which flow into the side channel ceased. The relation between discharge of the side channel and of the main channel is shown in Fig. 5.

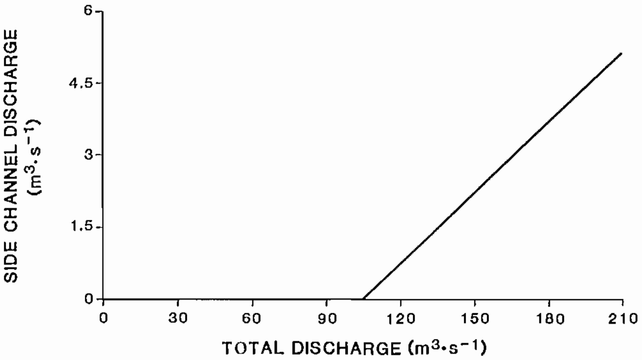

FIG. 5. Relation between total discharge and side channel discharge at Palisade site, Colorado River.

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[4] U.S. fish and Wildlife Service. 1985. Unpublished data. Regional Office, U.S. Fish and Wildlife Service, Denver, CO.

Once the stage-discharge relationship and the flow in the side channel are known, the rest of the analysis is comparatively simple. The discharges to be simulated in the side channel are determined from the empirical relation between main channel and side channel discharges (Fig. 5). The amount of microhabitat calculated for each of these discharges is weighted according to reach length, and added to similarly weighted values for the main channel at corresponding discharges. On the basis of predicted main channel water surface elevations and the inlet elevation at transect H, we determined that flow in the side channel ceases when the main channel discharge is less than 100 $m^3 \cdot s^{-1}$ Therefore, when one computes total reach habitat for lower discharges, zero flow would be simulated in the side channel.

The foregoing discussion concentrates on procedures for simulating low flows, but most microhabitat analyses also require attention to high flows. In a divided flow section, it is necessary to survey the bed cross section to the highest point on the island, to determine the flow at which the island becomes inundated. When that discharge is reached, the divided flow model no longer holds, and must be replaced by a single-channel model. Whereas different numbers of transects on either side of the island could be used for the divided flow model, the single-channel model requires that each transect be completed across the entire channel. At the Palisade site, the single channel model would require the extension of transects 6R through D, and the replacement of transects E through H. However, the characteristics of the main channel between transects 5 and 7 were highly uniform. The extension of the side channel cross sections could be performed with little more than a bed profile (which could be measured at any discharge) and a water surface profile that was measured at any discharge when the island was submerged. This combination is fortunate because hydrographic survey measurements under potentially dangerous high flow conditions are not required. The only critical high flow measurement is the water surface elevation, which can be taken near shore.

Tributary Backwaters — Although the analysis of many specialized microhabitat types can be similar to that used at the Palisade site, one type requires a different treatment. The mouths of tributaries are important microhabitat areas in some streams, and often function as refuges during extremely high or low flows. Treating these areas as independent stream reaches would seem to be a logical approach, except that they are not independent of the confluent stream. The stage in the tributary is often a function of the stage in the confluent stream, but the velocity distribution is more closely related to the discharge in the tributary. Occasionally the stage is not influenced by the confluent stream, but determined primarily by tributary discharge. Analysis of this type of variable backwater requires the development of a stage-discharge relation in the confluent stream, so that the backwater elevation in the tributary can be determined. A series of simulations is then conducted for the same tributary discharge, but with different starting water surface elevations corresponding to the discharge in the confluent stream. This procedure results in a family of habitat values, each depending on the discharge in both streams.

Habitat Dynamics

A feature of riverine environments is the seasonal, monthly, daily, and even hourly changes in the microhabitat quality and quantity. The most obvious change is complete dewatering. Beyond simple dewatering, the usability of the water column for a particular aquatic organism is very much a function of the temperature, fluid movement and hydraulics as expressed by point velocities and depths. Tracking of the quality of these microhabitats over time becomes a very important consideration in riverine fishery management.

Influence of River Hydrology

Streamflows in rivers vary from year to year and from day to day. The variation in habitat quality of a given river is related to the general climate pattern, the variation of runoff, and the nature of groundwater storage in the basin.

The typical approach to describing riverine hydrology is through the use of stream discharge monitoring at various points within a river basin. At these monitoring points, commonly referred to as "stream gaging stations," a river stage versus discharge relation is developed. Continuous records of stage are automatically recorded and later transformed into discharge values over the monitoring time period. For riverine fishery habitats, historical flow records over at least a 10-yr period are needed. Various hydrologic techniques are used to extend records from one part of a river basin to another and to synthesize records and fill data gaps.

Each river segment that has a unique flow pattern, therefore, needs a series of daily or monthly flow values that can be defined as a hydrologic baseline. Water management and development activities simulated with the aid of reservoir operating and water routing models can be used to create alternative hydrologic time series, for various water management options over this same historical "baseline" time period. These measured and synthesized hydrologic time series are typically summarized and presented as flow duration curves with daily, monthly, seasonal or annual time periods. Figure 6 is an example of a flow duration curve for

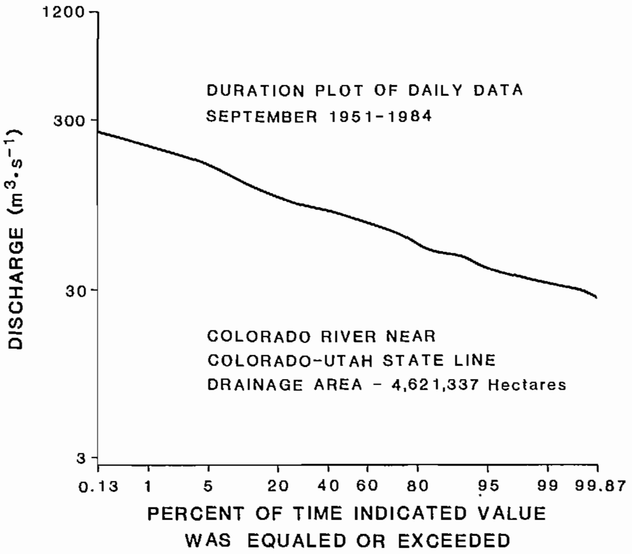

FIG. 6. Flow duration curve for month of September, stateline gage on Colorado River.

the month of September for the Colorado River near the stateline in Colorado.

Habitat Time Series

From time series and duration analyses, the water management community can determine the likelihood of given flow events occurring under various proposed regulation schemes. It therefore behooves the fishery manager to translate fishery habitat events into similar kinds of analyses. To do this for each river segment, one must first assemble flow-habitat functions such as those shown in Fig. 3 and 7, which represent the output from an instream water temperature macrohabitat model and the microhabitat model PHABSIM, respectively. With the hydrologic time series and the flow habitat functions, the dynamics of the physical habitat can be described for a specific river reach over time, while simultaneously illustrating various water management effects.

A generalized equation for the habitat versus streamflow function can be written as follows:

(4) $HA_t = f_i(Q_t)L$

where HA_t is the quantity of usable physical habitat, Q is the streamflow, and $f_i(Q)$ is the functional relation illustrated by Fig. 7. The subscript i refers to the specific fish species or life stage under investigation and L is the length of stream determined from a macro model (Fig. 3) to be represented by $f_i(Q)$ at time t.

From a time series of flows for a specific river segment (Q_t), the amount of usable physical habitat at time (t) can be calculated. The result of a unit length transformation of the $f_i(Q)$ function from Fig. 7 is illustrated in Fig. 8 for adult rainbow trout. The hydrologic time series for this river is also plotted in Fig. 8 for comparison. These time traces illustrate several important concepts that appear to be true for many fish species in many different types of streams: (1) the physical habitat time series is less variable than the streamflow time series; (2) high flow events may be as detrimental to fish as low flows; and (3) during some time periods, a moderate reduction in streamflow can result in a large reduction in physical habitat (e.g., compare August 1973 with August 1972) and other time periods when the converse is true (compare June 1971 with December 1973).

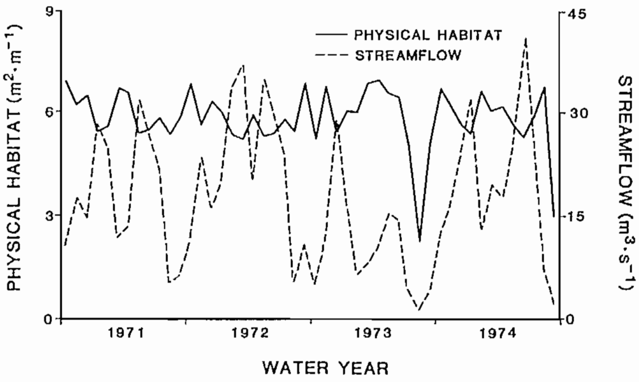

FIG. 7. Mean monthly streamflow and physical habitat for adult rainbow trout during 1971 through 1974 in the North Fork Snoqualmie River, Washington.

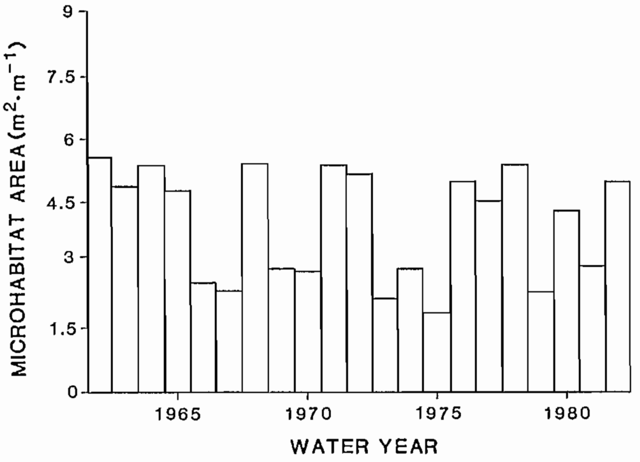

FIG. 8. Annual limiting microhabitat for adult rainbow trout in the North Fork Snoqualmie River, Washington.

Average monthly flow data were used to generate the habitat time series in Fig. 8. If daily flows were used and the habitat results averaged to arrive at the average monthly habitat values, the monthly values would not be the same. The habitat values for one water year, based on daily and monthly data, are compared in Table 2. The differences are not large for the North Fork Snoqualmie River; however, they still illustrate how important it is to use the same transformation procedure when comparing water management options such as those for pre- and post-project conditions. The choice between monthly or daily streamflow hydrological series depends on the objective of the analysis, available data, and funds. For example, daily values could be used for a gaged site where the water resources system is being simulated by using daily flows. In contrast, monthly streamflows would be used for a location with few existing streamflow measurements and where the streamflow record must be synthesized by regression with nearby sites.

Chronological time sequences are important for fishery studies because habitat analyses for all life stages are not applicable for every month of the year. For instance, rainbow trout spawning may occur from April to June. Spawn-

TABLE 2. Comparison of the results of different microhabitat generation procedures for adult brown trout (*Salmo trutta*) in the North Fork Snoqualmie River, Washington, October 1972 to September 1973.

Month	Daily streamflows	Monthly streamflows
	(Square metres per linear metre of stream)	
Oct.	4.85	5.34
Nov.	5.86	6.89
Dec.	5.52	5.52
Jan.	6.41	6.34
Feb.	5.80	6.16
Mar.	6.62	6.98
Apr.	6.74	7.08
May	6.53	6.50
June	6.53	6.59
July	4.79	5.19
Aug.	2.26	2.26
Sept.	3.48	4.79

ing habitat values are meaningless during the other months because the life stage is not present during those months. Juvenile and adult habitat, however, is needed throughout the year for a resident fish such as the rainbow trout. Consequently, hydrologic time series of monthly or daily values are needed for fishery studies, as opposed to the average annual flow values often used by water managers.

Effective Spawning and Incubation

Much research has been conducted on the size of gravel needed for spawning and the hydraulic conditions needed for redd building. Criteria for describing adequate depth, velocity, substrate, and percent fines in the interstitial spaces are available for several riverine salmonid species McMahon 1983; Baldrige and Amos 1981; Hickman and Raleigh 1982; Raleigh et al. 1983, 1984; Raleigh and Nelson 1985). Computer programs have been written to track the hydraulics above specified micro areas on river beds from the spawning through the incubation period (Milhous 1982a; Bovee 1985). From output of the PHABSIM microhabitat model, one can identify specific areas within a stream reach suitable for spawning. Even though spawning may have been successful in a given area of streambed, five events may occur that render it useless: (1) dewatering for 2 wk or longer during incubation; (2) freezing of embryos in shallow water; (3) scour — the resuspension of suitable size spawning gravel and its removal from the site; (4) deposition of fine materials within the interstitial spaces of the redd during the incubation period; and (5) movement of the redd gravels during the fry emergence period.

The effective spawning and incubation program simulates the hydraulic conditions over each of the suitable spawning areas for the several months of the incubation period and identifies the amount of the spawning area that is still intact at the computed time of hatching and emergence. Use of this program requires information about near bottom velocities that result in scour and deposition, and the depths at which dewatering or freezing occurs. The quantity of suitable microhabitat is determined by computing the surface areas having suitable conditions for both spawning and incubation for the period from spawning to hatching for each year in the time series. This can be repeated with simulated flow time series for a proposed water regulation scheme, and comparisons made. A variation of this type of analysis is possible when flow can be controlled by releases from a reservoir throughout the spawning and incubation period. Figure 9 shows a nomograph constructed for various incubation flows at a specified set of spawning flows in the Terror River, Alaska. From such nomographs, the best combination of spawning and incubation conditions can be determined for the amount of water that is forecasted to be available for management during a specific year.

Use of these engineering techniques, coupled with biological criteria makes it possible to illustrate impacts of alternative water management schemes. This capability can also be applied to real-time fishery management decisions. Water managers typically forecast water supply 1 to 6 months in the future and compare this with existing storage and the projected water supply and demand. The fishery manager can be effective, using the tools described here, and the forecasting capabilities of the water management engineers, to suggest that specific flows be maintained during the spawning season that are biologically compatible with the anticipated water supply during the incubation and hatching season. A common observation in rivers having uniform gravel bottoms is that fairly high flows during the spawning season result in the spawners building redds high up on the stream cross-section near the margins of the stream. Subsequently, if water supply drops, it may become impossible to maintain flows over these redds during the entire incubation period. If this could be forecasted, a better management scheme would be to reduce the flow during the spawning period, forcing the spawners lower into the channel where it is more probable that flows can be maintained during the incubation period. In other streams where spawning gravels may be limiting and control is feasible, the flow necessary to provide adequate conditions over the limited gravel bars can easily be computed and specified.

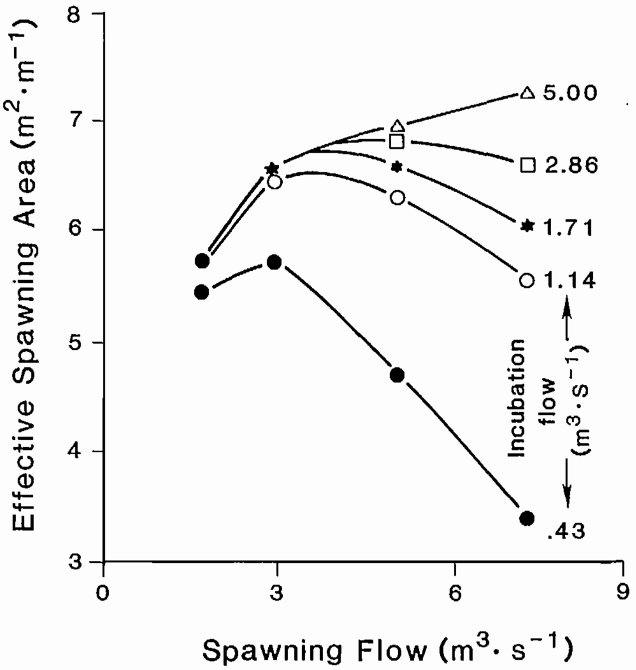

FIG. 9. The relation between effective spawning habitat area for pink salmon (*Oncorhynchus gorbuscha*) and spawning flow for specified incubation flows in Terror River, Alaska. Numbers at the end of each curve show incubation flow (from Milhous 1982a).

Temperature Analysis

It is well known that the length of the incubation period for salmonids is variable and is predominantly determined by the temperature of the water during the incubation period. The degree day accumulation (above a specified threshold temperature) for hatching has been well established for many salmonids (Piper et al. 1982). By using the degree-day output from a macrotemperature simulation one can derive the phenology of a species to determine the time of spawning, duration of incubation, and emergence. A hydrologic time series is used as input into the temperature model to yield degree-day simulations for various flow regulation schemes. For a particular species, the incubation period and hatching time is computed from the temperature degree-day simulation and used as input for the effective spawning and incubation analysis. Then, the physical microhabitat simulations and the effective spawning and incubation programs are used as discussed above to determine the composite areas suitable for spawning and incubation during the time period. Such composite simulations subsequently illustrate the general success for alternative water management schemes for each year across a given baseline hydrologic time series.

Channel Dynamics

As a subject of riverine habitat studies, channel morphology represents a variety of possible definitions. The physical configuration of a channel, both in cross section and plan view, is governed by several factors: the slope of the channel, the materials (including vegetation) through which the channel is cut, the size and volume of sediments delivered to the channel, and the streamflows that occur in the stream. A change in any of these variables has the potential to effect a change in the shape, pattern, or other physical characteristics of the stream.

In order to address the issue of channel morphology, one needs first to evaluate which of the aforementioned variables might change, and then, which avenues of analysis are applicable. In some studies, only the flow regime will be changed, and the investigator can address the issue by determining what flows would be needed to maintain the channel in its current configuration, the duration of such flows, and how often they need to be repeated. In other studies, only the volume of sediment input to the channel will be changed. In such cases, the channel may or may not shift to a different configuration, but the size of the substrate materials may be altered. This may dictate a focus upon altering discharge to cleanse the substrate rather than upon maintenance of channel morphology, per se. In other cases, several variables may be altered simultaneously, resulting in changes in channel dimensions, as well as substrate composition. Such cases cannot be addressed by a "channel maintenance" philosophy, and require an analysis of what the future channel may look like. These are typically much more complex problems than those concerned only with maintaining the status quo.

Channel Morphology

A variety of empirical relationships have been derived to address aspects of channel morphology with respect to individual variables. These relationships are sometimes referred to as regime equations. The most familiar of these are the hydraulic geometry relationships described by Leopold et al. (1964):

(5) $v = k\,Q^m$

(6) $d = c\,Q^f$

(7) $w = a\,Q^b$

where Q is a representative discharge for the stream, v is the average velocity at the discharge Q, d is the mean depth at the discharge Q, and w is the stream top width at the discharge Q. The terms k, m, c, f, a, and b are regression coefficients. When channel morphology has been considered in a riverine habitat study, the principal goal was usually to define a "channel maintenance" flow. The most common assumption made in determining this flow when a reservoir or diversion is proposed, is that the channel structure should be similar to that under pre-construction conditions while still maintaining the capacity of the stream to transport the annual sediment yield. The width and depth of a stream channel are often presented as power functions of a representative channel-forming discharge. The representative discharge (Q) most often used in these equations is the mean annual streamflow, the mean of a time series of annual peak flows, or the bankfull discharge. In many situations, the bankfull discharge is assumed to be the same as the annual peak flow with a return period of 1.5 yr. Nearly all of the existing methods for determining channel maintenance flows are based on equation 7. The Tennant method (Tennant 1976) indicates that a high flow of twice the mean annual flow, assumed to approximate bankfull discharge, is required to retain the same channel geometry.

An analytical procedure, following the same philosophy but not the same mathematical approach is described by the U.S. Forest Service (USFS 1986). This procedure was developed to estimate flow regimes that would be needed to preserve channel equilibrium if the volume of sediment entering the stream were unchanged.

The use of the annual peak flow with a return period of 1.5 yr is based on stream morphology studies in unregulated streams (Leopold et al. 1964). This approach is used in riverine habitat studies to maintain the state of dynamic equilibrium currently existing. In some cases, a change in this condition produces better habitat conditions for some species, whereas such changes in other systems are deterimental. Some forms of disequilibrium, such as aggradation, tend to be detrimental to many aquatic species. The principal advantage of the channel maintenance approach is that it attempts to keep a channel in its current configuration, so that the impacts of disequilibrium need not be addressed. Unfortunately, there are many instances where such channel modifications are unpreventable.

When it becomes necessary to consider changes in the channel morphology over time, we can reference the channel morphology equations to the existing conditions and rewrite them as follows:

(8) $$v = v_o \frac{Q^m}{Q_o}$$

(9) $$d = d_o \frac{Q^f}{Q_o}$$

(10) $$w = w_o \frac{Q^b}{Q_o}$$

where the subscript o refers to the existing conditions.

If the assumption is made that the channel-forming discharge is the 1.5 yr or the mean annual peak flow, there will be no change in velocity, depth, and width — in other words no change in the channel morphology — when there is no change in the 1.5 year or mean annual peak flow. Values of the power coefficients for equations 8, 9, and 10 are shown for three streams in Table 3. Calculated changes in average velocity, depth, and width as a function of an assumed reduction of the peak annual flow are provided in Table 4.

Many regime equations are derived through univariate regression analysis. This means that, in general, one could expect about the same regression slopes provided that there is some degree of similarity among the streams measured. The agreement among the coefficients in Table 3 may seem

TABLE 3. Power coefficients in certain channel morphology relations.

Coefficient	Kansas[a]	Alberta[b]	Salmon River, ID[c]	Average
m	0.16	0.14	0.12	0.14
f	0.31	0.33	0.34	0.33
b	0.54	0.53	0.54	0.54

[a] Streamflow exceeded 10% of the time (from Burns 1971).
[b] Two-year flood flow (from Bray 1982).
[c] Annual peak with a 1 in 2-yr return period (from Emmett 1975).

TABLE 4. Percent decrease in certain characteristics of stream morphology resulting from reduction of peak streamflows.

Morphology factor	Power[a] coefficient	Percent reduction in peak flow		
		10	33	50
Velocity	0.14	1.5	5.5	9.2
Depth	0.32	3.3	12.2	19.2
Width	0.54	5.5	19.6	31.2
Width/depth	0.22[b]	2.2	8.5	14.1

[a] From Table 3.
[b] Coefficient for width minus coefficient for depth.

remarkable, considering the geographic diversity of the streams. However, when regressions are performed on streams conforming to a different set of conditions, different relationships could be anticipated.

Whereas hydraulic geometry equations might be predictive in a situation where only the flows changed, they would not be well suited to an application where both the flow and the sediment load were modified. This concept is illustrated in Table 5, based on data from the North Platte River and the Platte River in Nebraska (Williams 1978). In this case, the change in width is greatly underestimated, most likely because the analysis did not account for a change in sediment load and size nor the encroachment of riparian vegetation.

Using the results of a laboratory study by Raju et al. (1977) for variable sediment discharge and constant water discharge we obtained the following relations:

(11) $v = Q_s^{0.10}$
(12) $d = Q_s^{-0.12}$
(13) $w = Q_s^{0.02}$
(14) $S = Q_s^{0.43}$
(15) $w/d = Q_s^{0.13}$

where S is the slope, and Q_s is the sediment discharge; the other terms as defined previously. The study was made at nearly constant discharge and used particles ≤ 0.27 mm in diameter.

Three interesting points were developed in this study: (1) the major impact of a change in the sediment load with no change in streamflow was on the slope; (2) the width did not change significantly with a change in sediment load; and (3) the depth decreased with an increase in sediment load.

In most rivers, the slope cannot increase without the river becoming straighter. Sinuosity — the ratio of the channel length to the valley length — decreases with an increase in sediment load. In addition, the meander wave length increases.

Schumm (1977) suggested the following generalized relationships:

(16) $Q = f_1$ (width, depth, meander wave length, 1/slope)
(17) $Q_s = f_2$ (width, 1/depth, meander wave length, slope, 1/sinuosity)

where Q is the streamflow and Q_s is the sediment load.

In many water development projects, both the sediment load and the streamflow may be changed. The direction of change suggested by Schumm (1977) is illustrated in Table 6 to show channel changes expected from specified changes in sediment loads and streamflow.

When a reservoir is constructed, the impact on both the sediment load and the peak flows is significant. From Table 6 we would expect the width of a river to decrease after decreasing both the discharge and sediment load. Actual results from 16 projects (Table 7), illustrate some inconsistencies with these generalities. The width *increased* in 11 (which is not the expected change) and decreased is 5 (the expected result).

Hay (1982) provided the following equations to use with mobile gravel bed rivers.

(18) $P = 2.20\ Q^{0.54}\ Q_s^{-0.05}$
(19) $R = 0.161\ Q^{0.41}\ D_{50}^{-0.15}$
(20) $d_m = 0.252\ Q^{0.38}\ D_{50}^{-0.16}$
(21) $S = 0.679\ Q^{-0.53}\ Q_s^{0.13} D_{50}^{0.97}$

TABLE 5. Comparison of estimated vs. observed change in channel width of the North Platte and Platte rivers, Nebraska, using the hydraulic geometry equations.

	Base condition		Modified condition			Ratio:
Location	Mean peak flow[a] ($m^3 \cdot s^{-1}$)	Width (m)	Mean peak flow[b] ($m^3 \cdot s^{-1}$)	Estimated[c] width	Observed width	Actual/ estimated
Sutherland	152	410	68	265	75	0.28
North Platte	217	520	72	282	90	0.32
Brady	218	340	100	223	45	0.20
Cozad	204	440	84	324	40	0.12
Overton	293	1 520	140	1 020	335	0.33
Odessa	196	930	165	506	490	0.95
Grand Island	312	730	174	545	760	1.39

[a] Peaks between July 1927 and March 1939.
[b] Peaks between October 1957 and 1970.
[c] Estimated width = width (1938) × (Q(1965)/Q(1938)) exp. 0.54. Data source: Williams (1978).

TABLE 6. Changes in channel morphology resulting from alterations in stream flow and sediment yield.[a]

Independent variable		Dependent variable					
Stream discharge	Sediment load	Channel width	Average channel depth	Meander wave length	Channel scope	Ratio of valley slope to channel slope	Ratio of width to depth
+	NC	+	+	+	−	−	−
−	NC	−	−	−	+	+	+
NC	+	+	−	+	+	−	+
NC	−	−	+	−	−	+	−
+	+	+	±	+	±	+	−
−	−	−	±	−	±	+	−
+	−	±	+	±	−	+	−
−	+	±	−	±	+	−	+

[a]NC = no change; + = direction of change is an increase; − = direction of change is a decrease; ± = direction of change is indeterminant.(Modified from Schumm 1977.)

TABLE 7. Change in width resulting from construction of a dam and reservoir.[a]

River	Average width (m)		Average annual peak discharge ($m^3 \cdot s^{-1}$)	
	Pre-dam	Post-dam	Pre-dam	Post-dam
Chattahoochee River, GA	69.2	70.6	660	270
Jemez River, NM	213	46	160	39
Arkansas River, CO	152	45	560	190
Missouri River, MT	272	315	770	690
Missouri River, ND	568	727	3 900	1 100
Missouri River, SD	707	826	5 200	1 200
Medicine Creek, NE	53	56	530	13.5
Middle Loup River, NE	33	77	58	53
Smoky Hill River, KS	39	40	320	135
Republican River, KS	127	140	290	150
Wolf Creek, OK	223	31	240	35
North Canadian River, OK	52	28	280	44
Canadian River, OK	369	357	3 600	740
Red River, OK-TX	255	268	3 000	950
Nueces River, TX	106	126	1 100	800
Des Moines River, IA	168	177	1 200	800

[a]Source: William and Wolman (1984).

where Q = the 1.5 yr annual flood flow in m^3/s, Q_s = the bed load in m^3/s, D_{50} = the median particle size of the bed material (m), P = the wetted perimeter (m), R = the hydraulic radius (m), d_m = the maximum flow depth (m), and S = slope.

The Hay equations demonstrate that changes in channel geometry can result from changes in sediment loads, streamflow, or the size of the sediment load, and not just streamflow alone. Lane (1955) gave the following equation to elucidate some of the possible changes.

(22) $Q_sD \backsim Q_w52$

where Q_s is the bed material load, Q_w is the streamflow, D is the size of the bed material, and S is the slope of the stream.

Use of hydraulic geometry equations for channel maintenance should be restricted to water planning studies for the purpose of reserving flows from future consumptive uses, where the assumption is being made that the channel must remain the same as presently exists. These equations are not appropriate for impact analyses and the management of regulated rivers which will alter both flow and sediment transport. A further restriction is that the equations apply only to alluvial rivers, which means that the river bed and banks are composed of sediments and are not controlled by bedrock.

The alternative to maintaining the existing channel is to predict the channel characteristics resulting from the streamflows and sediment movement from specific water resources development. A basic assumption of physical process models is that the nature of a stream channel, including the bed material, is related to *all* the flows that occur in the channel and that the channel is in a continuous process of adjustment. Consequently, a new pattern of flows may produce a channel response even though the bankfull discharge may remain the same.

The linking of physical fish habitat analyses to stream sedimentation processes modeling is of considerable importance and a high priority subject for additional research if we are to have any influence upon how streams are to be managed. Sedimentation models such as HEC-6 (Hydrological Engineering Center 1976) have been developed to simulate the change in channel form as a function of streamflow over time. Predictions of channel response to changing flow regimes can be simulated fairly well in alluvial sand bed streams by using HEC-6, but the HEC-6 model cannot yet provide reasonable results in gravel-bed rivers. Improved transport functions for gravelbed streams need to be developed. See Milhous et al. (1986) for a discussion of this problem.

Using physical process models, it will be possible to determine:

- changes in stream bed elevations in sand bed streams due to alterations of sediment supply and/or flow regime.
- flushing flows for removal of fines from the bed material in gravel bed streams
- flow required to remove sprouting vegetation from bend and point bars.
- flows required to transport sediment delivered to a river segment by increased sediment production from upstream sources such as tributaries.

Flushing Flows

In the normal course of events, in unregulated rivers, fines are deposited in and on the gravel substrate during low flows and are resuspended from the gravel substrate during higher flows. In many regulated rivers, this flushing of fines either does not occur or occurs infrequently. The purpose of a "flushing flow" management scheme, therefore, is to maintain the substrate in a healthy condition during biologically critical times of the year. Most authors, when discussing flow methods, have interchanged channel maintenance and flushing concepts.

Flushing flows are of most concern in gravel-bed streams that transport fines in suspension. Many of the aquatic organisms in a gravel bed river require a clean gravel substrate for some of their life processes. For example, gravel is used for spawning and egg incubation by trout and salmon. As the interstitial spaces or voids fill with fines, many of these life processes cannot continue.

Rieser et al. (1985) have recently reviewed flushing flow requirements for stream fishes, the stream flows required to maintain relatively silt free surface or interstitial spaces in gravel bed substrates. Typically, the necessity for regulated flushing flows occurs below a reservoir with sufficient capacity to significantly reduce peak flood flows, alter sediment transport, or both.

Milhous (1982b) and Milhous et al. (1986) postulated two general processes for deposition of fine material in gravel streams. The first assumes that fines are deposited predominantly on the surface and the second that they are deposited within the interstitial voids of the gravel particles and must be periodically resuspended. Flushing flows for both involve a movement parameter, β defined as follows:

$$\beta = \frac{RS}{(G_s - 1)D_{50}} \qquad (23)$$

where R = the hydraulic radius, S = the energy slope, G_s = the specific gravity of the bed material, and D_{50} = the median particle size of the bed surface material (armor layer)

Field observations suggest that the bed surface needs only to be slightly disturbed to move fines from the surface. This movement has been found to occur at a β value of 0.021 (Milhous et al. 1986). In contrast, the armor particle on the bed surface would have to be moved significantly to remove fines from the voids within the gravel. Milhous et al. (1986) recommended a β value of at least 0.030, and preferably 0.035, for interstitial flushing in streams which tend to armour. The relation between the movement parameter β and discharge, in the Williams Fort River, Colorado, is given in Fig. 10. Using β values of 0.021 and 0.035, respectively, Fig. 10 indicates that surface flushing occurs at about 7.1 $m^3 \bullet s^{-1}$ and interstitial flushing at about 18.3 $m^3 \bullet s^{-1}$.

Unless the watershed upstream is disturbed, the Williams Fork River should require only periodic surface flushing, because the suspended sediment load is small and the suspended particles are relatively large, judging by watershed geology. It must be emphasized, however, that a flushing flow has a different purpose than a channel maintenance flow. A discharge of 7.1 $m^3 \bullet s^{-1}$ may keep the streambed clean, but may not be sufficient to scour out pools, prevent vegetation encroachment, or avoid disequilibrium. It is more likely that a higher flow would be needed to maintain the current channel configuration at current rates of sediment input. If sediment were totally interrupted, then a flow of 7.1 $m^3 \bullet s^{-1}$ would be more appropriate, although the stream dimensions would probably shift to fit this new dominant discharge. In this case, a decision must be made as to which is more important to preserve: channel dimensions or substrate composition. Under this scenario, it is unlikely that both can be achieved.

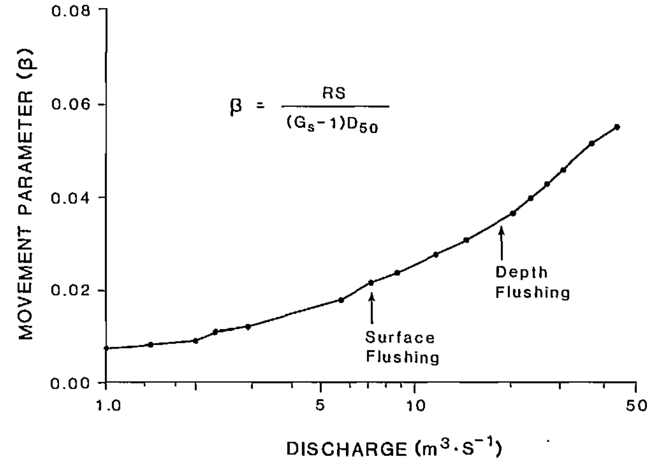

FIG. 10. Movement parameter (β) versus discharge in the Williams Fork River, Colorado (from Milhous et al. 1986).

Conclusions

Habitat analyses in large and small rivers have many common elements, which may give the appearance that the same procedures are followed, regardless of stream size. Certain aspects of these studies, such as hydraulic simulation, may actually be easier in large rivers because the hydraulic characteristics are often less variable over time and space. Closer examination reveals that there are numerous critical distinctions between large and small river habitat analyses.

One of the most important size-related differences is the simulation of nose velocities, rather than mean column velocities for demersal species. If the subject species occupies a mid-column position or is pelagic, there may be little difference between the mean column and nose velocities. However, simulation of mean column velocities for a demersal species can have two detrimental results. First, there will be an overall tendency for the amount of available habitat to be underestimated for the higher flows, because the mean column velocity will consistently be too fast for the fish. Second, when usable microhabitat is plotted against discharge, the resulting curve will peak at a relatively low discharge, and will decrease rapidly at higher flows. Use of nose velocities typically results in a more robust habitat vs. discharge relationship (i.e., a broader curve) which may peak at a higher flow than one based on mean column velocities.

We have avoided a definition of what differentiates a large river from a small one. Many investigators would probably make this distinction on the basis of channel width, mean annual discharge, drainage area, or some other size-related characteristic. Based on the foregoing discussion, the best distinguishing characteristic may be channel depth, as this will determine the vertical location of the mean column velocity measurement. When measuring stream velocities, as a rule of thumb, hydrologists change from a single measurement at 0.6 of the depth to an average of two measurements at 0.2 and 0.8 of the depth, when the depth exceeds about 1 m. Therefore, it is suggested that whenever the depth exceeds one meter, nose velocities be used instead of mean column velocities, and that this is one criterion differentiating small from large rivers. Based on this standard, there are relatively few small streams in North America.

However, there is one other characteristic that distinguishes truly large rivers — the relative importance of specialized or isolated habitat types associated with the river margin. In small and medium-sized streams, the same species is found at suitable locations throughout the stream. There may be much more habitat partitioning in larger rivers, with certain species associated only with edge habitats, and others found almost exclusively in mid-stream. It should be noted that this tendency is related more to the combined effects of physical and hydraulic structure than to the size of the channel. If a stream that would otherwise be classified as large has the same structural diversity of a small stream, the same species will probably be scattered throughout the channel. However, many large rivers tend to have a definite zonation, consisting of a hydraulically efficient (and often biologically devoid) main channel, and the biologically rich zones associated with the edges. In contrast, the biologically rich zones tend to overlap in small rivers.

In many large rivers, the role of streamflow in the main channel is little more than providing water to the zones occupied by the fish. The determination and simulation of flow-induced habitat fluctuations in these specialized habitat areas provides the challenge in large-river investigations, because of their tendency to be hydraulically controlled by a variable backwater. The hydraulic complexities of these areas can prove to be difficult to simulate, but are rarely insurmountable. The more perplexing problem is that many instream flow investigators do not (or cannot) recognize variable backwaters when they see them. This emphasizes the advantage of including expertise in hydraulics, hydrology, and biology on any riverine habitat analysis team.

The determination of instream flow requirements to provide suitable habitat for fishes can be assisted by use of physical habitat versus streamflow functions and the analysis of instream benefits produced by alternative flow regimes. These can be compared to benefits from diversionary uses in order to obtain a reasonable mix of uses as the goal of the allocation of the water resource.

If a habitat versus streamflow relationship is used as a surrogate production function, a water management project can be formulated to include instream flows as an equal among various project purposes in the overall project production function (Milhous 1983). In contrast, if the function is used only for the evaluation of impacts, the resulting instream flow requirements are treated as constraints on the allocation of water to ''useful'' purposes (Henrikson 1980; Hoffman 1980; Christiano[5]). The use of the habitat-streamflow function in a reservoir analysis was given by Milhous (1982a), Sale et al. (1982), and Olive and Lamb (1984).

References

Annear, T. C., and A. L. Conder. 1984. Relative bias of several fisheries instream flow methods. N. Am. J. Fish. Manage. 4: 531–539.

American Society of Civil Engineers. 1962. Nomenclature of hydraulics. ASCE manuals and reports on Engineering Practice No. 43. New York, NY. 501 p.

Baldrige, J. E., and D. Amos. 1981. A technique for determining fish habitat suitability criteria: a comparison between habitat utilization and availability, p. 251–258. *In* N. B. Armentrout [ed.] Acquisition and utilization of aquatic habitat inventory information. Am. Fish. Soc., Bethesda, MD.

Binns, N. A., and F. M. Eiserman. 1979. Quantification of fluvial trout habitat in Wyoming. Trans. Am. Fish. Soc. 108: 215–228.

Bovee, K. D. 1982. A guide to stream habitat analysis using the instream flow incremental methodology. Instream Flow Information Paper No. 12. U.S. Fish Wildl. Serv. FWS/OBS-82/26. 248 p.

1985. Evaluation of effects of hydropeaking on aquatic macroinvertebrates using PHABSIM, p. 236–241. *In* F. W. Olson, R. G. White, and R. H. Hamre [ed.] Proc. Symp. on small hydropower and fisheries. Am. Fish. Soc., Bethesda, MD.

1986. Development and evaluation of habitat suitability criteria for use in the instream flow incremental methodology. Instream Flow Information Paper No. 21. U.S. Fish Wildl. Serv. Biol. Rep. 86(7): 235 p.

Bray, D. I. 1982. Regime equations for gravel-bed rivers, p. 517–542. *In* R. D. Hay, J. C. Bathurst, and C. R. Thorne [ed.] Gravel-bed rivers. John Wiley and Sons, London.

Brungs, W. A., and B. R. Jones. 1977. Temperature criteria for freshwater fish: protocol and procedures. U.S. Environmental Protection Agency, Ecol. Res. Series. EPA-600/3-77-061.

Burns, C. V. 1971. Kansas streamflow characteristics, Part 8, In-channel hydraulic geometry of streams in Kansas. Kansas Water Resour. Bd., Tech. Rep. 8.

Cairns, J., Jr. 1968. Suspended solids standards for the protection of aquatic organisms. Purdue Univ. Eng. Bull. 129(1): 16–27.

---

[5] Christiano, D. J. 1981. Negotiating for instream water. Presented at the 1981 Conference of the American Water Works Association, St. Louis, MO, USA.

Chow, V. T. 1959. Open-channel hydraulics. McGraw-Hill, New York, NY. 680 p.

Carter, R. W., and J. Davidian. 1968. General procedure for gaging streams. U.S. Geol. Surv. Tech. For. Water-Res. Invest. of U.S. Geol. Surv. Book 3, Chap. A6. 13 p.

Collings, M. R. 1972. A methodology for determining instream flow requirements for fish. Proceedings of Instream Flow Methodology Workshop. Washington State Department of Ecology, Olympia, WA. 130 p. + appendix.

Coutant, C. C. 1977. Compilation of temperature preference data. J. Fish. Res. Board Can. 36: 366–376.

Dunne, T., and L. B. Leopold. 1978. Water in environmental planning. W. H. Freeman and Co., San Francisco, CA. 818 p.

Emmett, W. W. 1975. The channel and waters of the upper Salmon river area, Idaho. U.S. Geol. Surv. Prof. Paper 870-A: 116 p.

Everest, E. H. and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenille chinook salmon and steelhead trout in two Idaho streams. J. Fish. Res. Board Can. 29: 91–100.

Fauch, K. D., C. L. Hawkes, and M. G. Parsons. 1988. Models that predict standing crop of stream fish from habitat variables: 1950–85. Gen. Tech. Rep. PNW-GTR-213. Portland, OR; U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 52 p.

Fritschen, J. A., R. T. Milhous, and J. Nestler. 1984. Measuring resource potential for river recreation, p. 484–494. *In* J. S. Popadic, D. I. Butterfield, D. H. Anderson, and M. R. Papodic [ed.] Proc. 1984 Nat. Riv. Rec. Symp., Baton Rouge, LA.

Hay, R. D. 1982. Design equations for mobile gravel-bed rivers, p. 553–574. *In* R. D. Hay, J. C. Bathurst, and C. R. Thorne[ed.] Gravel-bed rivers. John Wiley and sons, London.

Henriksen, J. 1980. Stipulation of instream flow regime in Section 404 permit conditions. Proc. Ann. Conf. West. Assoc. Fish Wildl. Agencies. 60: 389–395.

Hickman, T. J., and R. F. Raleigh. 1982. Habitat suitability index models: cutthroat trout. U.S. Fish Wildl. Serv. FWS/OBS-82/10.5: 38 p.

Hoffman, J. P. 1980. Determining optimum release from Lewiston Dam to improve salmon and steelhead habitat in the Trinity River, California. Proc. Ann. Conf. West. Assoc. Fish Wildl. Agencies. 60: 366–388.

Hydrologic Engineering Center. 1976. HEC-6: Scour and deposition in rivers and reservoirs, users manual. Hydrologic Engineering Center, U.S. Army Corps of Engineers, Davis, CA. 34 p. + exhibits.

Hynes, H. B. N. 1970. The ecology of running waters. Liverpool Univ. Press, Liverpool, England. 555 p.

King, H. W., and E. F. Brater. 1963. Handook of hydraulics. McGraw-Hill, New York, NY. 565 p.

Lane, E. W. 1955. The importance of fluvial morphology in hydraulic engineering. Proc.-ASCE, Paper 795, Vol. 81.

Leopold, L. B., W. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. Freeman and Sons, San Francisco, CA. 522 p.

Loar, J. N., and M. J. Sale. 1981. Analysis of environmental issues related to small-scale hydroelectric development: instream flow needs for fishery resources. Oak Ridge Nat. Lab., Environ. Sci. Publ. 1929: 90 p.

McMahon, T. E. 1983. Habitat suitability index models: coho salmon. U.S. Fish Wildl. Serv. FWS/OBS-82/10.49: 29 p.

Milhous, R. T. 1979. The PHABSIM system for instream flow studies, p. 440–446. *In* Proc. 1979 Summer Computer Simulation Conf., Toronto, Ontario. Society for Computer Simulation, La Jolla, CA.

1982a. Quantifying instream values for water allocations, p. 489–494. *In* F. Kilpatrick and D. Matchett [ed.] Proc. conf. water and energy tech. policy issues. ASCE, Bethesda, MD.

1982b. Effect of sediment transport and flow regulation on the ecology of gravel bed rivers, p. 819–841. *In* R. D. Hayes, T. C. Bathurst, and C. R. Thorne [ed.] Gravel-bed rivers. John Wiley and Sons, London.

1983. Instream flow values as a factor in water management, p. 231–237. *In* R. J. Charbeneavo and B. P. Popking [ed.] Regional and state water resources planning and management. Proc. Am. Water Res. Assoc., Bethesda, MD.

Milhous, R. T., D. L. Wegner, and T. W. Waddle. 1984. User's guide to the Physical Habitat Simulation System. Instream Flow Information Paper No. 11. U.S. Fish Wildl. Serv. FWS/OBS-81/43: 312 p.

Milhous, R. T., J. B. Bradley, and C. L. Loeffler. 1986. Sediment transport simulation in an armoured stream, p. 116–126. *In* Proc. 4th Fed. Interagency Sed. Conf., Vol. 2.

Morhardt, J. E. 1986. Instream flow methodologies. Electric Power Res. Inst. EA-4819, Res. Proj. 2194-2, Palo Alto, CA. 302 p. + appendix.

Morisawa, M. 1968. Streams: their dynamics and morphology. McGraw-Hill, New York, NY. 175 p.

Olive, S. W., and B. L. Lamb. 1984. Conducting a FERC environmental assessment: a case study and recommendations for Terror Lake Project. U.S. Fish Wildl. Serv. FWS/OBS-84/08: 62 p.

Piper, R. G., I. B. McElwain, L. E. Orme, J. P. McCraren, L. G. Fowler, and J. R. Leonard. 1982. Fish hatchery management. U.S. Fish Wildl. Serv., Washington, DC. 517 p.

Raleigh, R. F., L. D. Zuckerman, and P. C. Nelson. 1983. Habitat suitability information: brown trout. U.S. Fish Wild. Serv. FWS/OBS-82/10.71: 71 p.

Raleigh, R. F., T. Hickman, R. C. Solomon, and P. C. Nelson. 1984. Habitat suitability information: rainbow trout. U.S. Fish Wildl. Serv. FWS/OBS-82/10.60: 64 p.

Raleigh, R. F., and P. C. Nelson. 1985. Habitat suitability index models and instream flow suitability curves: pink salmon. U.S. Fish Wildl. Serv. Biol. Rep. 82(10.109): 36 p.

Raju, K. G. R., K. R. Ohandapani, and D. M. Kondap. 1977. Effect of sediment load on stable sand canal dimensions. Journal of the Waterway, Port, Coastal, and Ocean Division. ASCE 103(WWZ): 241–249.

Reiser, D. W., M. P. Ramey, and T. R. Lambert. 1985. Review of flushing flow requirements in regulated streams. Dep. Eng. Res. Pacific Gas and Electric Co., San Ramon, CA. 97 p. + 4 appendices.

Sale, M. J., E. D. Brill, Jr., and E. E. Herricks. 1982. An approach to optimizing reservoir operation for downstream aquatic resources. Water Resour. Res. 18(4): 705–712.

Schlichting, H. 1968. Boundary Layer Theory. Sixth ed. McGraw-Hill, New York, NY.

Schumm, S. A. 1977. The fluvial system. John Wiley and Sons, New York, NY. 338 p.

Stalnaker, C. B. 1979. The use of habitat preferenda for establishing flow regimes necessary for maintenance of fish habitat, p. 321–337. *In* J. V. Ward and J. A. Stanford [ed.] The ecology of regulated streams. Plenum Publ. Corp., New York, NY.

Tennant, D. L. 1976. Instream flow regimes for fish, wildlife, recreation, and related environmental resources, p. 359–373. *In* J. Orsborn and C. Allman [ed.] Proc. Spec. Conf. on instream flow needs, Vol. II. Am. Fish. Soc., Bethesda, MD.

Theurer, F. D., K. A. Voos, and W. J. Miller. 1984. Instream water temperature model. Instream Flow Information Paper No. 16, U.S. Fish Wildl. Serv. FWS/OBS-84/15: 372 p.

THEURER, F. D., C. G. PREWITT, AND K. A. VOOS. 1982. Application of IFG's instream water temperature model in the upper Colorado River, p. 287-292. *In* A. Johnson and R. Clark [ed.] Proc. Internat. Symp. Hydrometeorology. Am. Water Resour. Assoc., Bethesda, MD.

TRIHEY, E. W., AND C. B. STALNAKER. 1985. Evolution and application of instream flow methodologies to small hydropower development: an overview of the issues, p. 176-183. *In* F. W. Olson, R. G. white, and R. H. Hamre [ed.] Proc. Symp. on small hydropower and fisheries. Am. Fish. Soc., Bethesda, MD.

TYUS, H. M., B. D. BURDICK, AND C. W. MCADA. 1984. Use of radiotelemetry for obtaining habitat preference data on Colorado squawfish. N. Am. J. Fish. Manage. 4: 177-180.

U.S. FISH AND WILDLIFE SERVICE. 1980. Habitat evaluation procedures. U.S. Fish Wildl. Serv. ESM 102. unpaginated.

U.S. FOREST SERVICE. 1986. Procedure for quantifying channel maintenance flows, Chap. 30. *In* Forest Service Handbook FSH2509.17, Water Information System Handbook. U.S. Forest Serv., Washington, DC.

WESCHE, T. A., AND P. A. RECHARD. 1980. A summary of instream flow methods for fisheries and related research needs. Eisenhower Consortium Bulletin No. 9. Eisenhower Consortium for Western Environmental Forestry Research, U.S. Government Printing Office, Washington, DC. 122 p.

WILLIAMS, G. P. 1978. The Case of the Shrinking Channels — the North Platte and Platte Rivers in Nebraska. U.S. Geol. Surv. Cir. 787. 48 p.

WILLIAMS, G. P., AND M. G. WOLMAN. 1984. Downstream effects of dams on alluvial rivers. U.S. Geol. Surv. Prof. Paper 1286: 83 p.

WINGER, P. V. 1980. Physical and chemical characteristics of warmwater streams: a review, p. 32-44. *In* L. A. Krumholz [ed.] Warmwater Streams Symp. Southern Div. Am. Fish. Soc., Allen Press Inc., Lawrence, KS.

The Morphology of Large Rivers: Characterization and Management

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Abstract

KELLERHALS, R., AND M. CHURCH. 1989. The morphology of large rivers: characterization and management, p. 31–48. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The study of fluvial morphology has emerged as an important topic since the detrimental effects upon aquatic resources of river development have become apparent. In this paper, recent morphological classification concepts are introduced to develop a common terminology amongst geomorphologists, biologists and engineers. Factors and processes that determine fluvial morphology are reviewed to indicate our present capacity to understand and predict morphological changes caused by human interference in rivers. The principal factors governing the morphology of alluvial channels are streamflow, sediment load, and physiographic setting and history. A summary table is given of the trends that may be expected to follow changes in discharge, bed material sediment load, and wash material sediment load of the river. The "hydraulic geometry" of river channels is presented as a description of the geophysical basis of riverine habitat. Principles are illustrated by case studies from western Canada including effects produced by interbasin water diversion and flow regulation by large dams.

Résumé

KELLERHALS, R., AND M. CHURCH. 1989. The morphology of large rivers: characterization and management, p. 31–48. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

L'étude de la morphologie fluviale est apparue comme un sujet important depuis que les effets nuisibles pour les ressources aquatiques de l'aménagement des cours d'eau sont devenus apparents. Dans cet article, on présente des concepts récents de classification morphologique dans le but d'élaborer une terminologie commune aux géomorphologistes, biologistes et ingénieurs. On examine les facteurs et les mécanismes qui déterminent la morphologie fluviale pour montrer notre capacité actuelle de comprendre et de prédire les changements morphologiques dus à l'intervention de l'homme dans les cours d'eau. Les principaux facteurs qui régissent la morphologie des lits non consolidés sont le débit, la charge sédimentaire ainsi que l'état et l'histoire physiographiques. On trace un tableau sommaire des tendances qui pourraient faire suite à des modifications du débit, de la charge sédimentaire des matériaux du lit et de la charge sédimentaire des matériaux lessivés. La « géométrie hydraulique » de lits de cours d'eau est présentée comme décrivant la base géophysique de l'habitat riverain. Les principes sont illustrés au moyen d'études de cas dans l'ouest canadien y compris les effets produits par la dérivation de l'eau entre des bassins et la régularisation du débit par de grands barrages.

Introduction

Rivers and the nearby land shaped by the river exhibit a bewildering array of landforms. Fluvial geomorphology is the branch of science that attempts to find some systematic order in this suite of landforms and tries to understand the processes responsible for its development. The fluvial landscape, or at least some major parts of it, have less permanence than most other landscapes on earth, and are readily and often unwittingly affected by the activities of man. This, combined with the fact that these changes can have far-reaching economic and ecological consequences, justifies the present great interest in developing a better understanding of the processes that are responsible for creating and changing riverine landscapes.

Engineering interest in fluvial morphology is relatively new and has originated mainly with a gradual realisation of just how much useful management and design information can be extracted from a careful interpretation of various morphological features. Since these features are a record of the river's past performance, they often provide far more reliable data than short-term standard engineering measurements. More recently yet, documented case histories of morphologic changes due to various actions of man have begun to appear. In some cases the morphologic changes have had seriously detrimental effects on resources such as fish, wildlife, recreation, navigation, or the quality of the water itself. As a consequence, fluvial morphology is no longer just a tool for the study of other engineering matters, but it has become a subject of direct interest to engineers, fisheries biologists and others interested in river management.

From a fisheries perspective, the morphology of a river directly determines the prevailing distribution of depth, velocity and substrate. In a broader sense, it provides the physical framework within which all aspects of habitat must fit.

This paper is intended to review the subject for specialists in related fields such as fisheries or water resources management. Specific objectives are: (i) to introduce some recent morphological classification concepts so as to develop a common terminology; (ii) to discuss the factors and processes that determine fluvial morphology; (iii) to illustrate our present capabilities to understand and predict morphological changes due to human interference, on the basis of some Canadian case histories; and (iv) to examine data needs and make a plea for better monitoring of critical morphological parameters.

The literature on fluvial morphology is extensive. In the last few years there has been an annual crop of several massive conference proceedings addressing aspects of fluvial processes and morphology, and a spate of new textbooks. A brief paper clearly cannot present the details of such a subject, but we hope that the paper will serve as a basis for informed discussion.

River morphology and morphologic changes are the result of many interacting fators and processes, most of which are themselves subject to change on a wide range of time scales, from hours in the case of local discharge and sediment transport to thousands of years for neotectonic activity or sea level changes.

The essential determining factor of local river morphology is the supply of water from upstream. It may or may not be accompanied by sediment. The time distribution of the water supply, the local geologic history and some actions of man are other primary factors. Local climate, vegetation, and riparian land use are secondary factors that can be important.

Clearly, most of these factors are subject to change along a river. Such changes may be subtle, as a major river gradually grades into a tide-dominated estuary, or they may be drastic and abrupt, as a mountain river suddenly drops into a bedrock canyon after a long gentle reach across an infilled lake basin. Clearly, before trying to classify a river, it has to be divided into reasonably homogeneous units, the so-calles "reaches". This can normally be done *a priori* on airphotos and maps. Most reach breaks are located at obvious sites, such as tributary confluences, bedrock sills, canyon entrances and exits, and lakes, but there are less obvious reach breaks, associated with changes in geologic history or valley floor materials, that may not become apparent until considerable study has been undertaken.

From a fishery management perspective, morphologic changes are a critically important aspect of fluvial morphology. Natural effects such as climatic change, neotectonics, and singular events such as landslides bring about changes, but the most rapid and dramatic changes have, by and large, been man-induced. The latter part of this paper is devoted to providing some guidance to what is, and what is not predictable.

Throughout this paper we interpet "large rivers" to mean ones unlikely to be ordinarily affected locally by blockage across a substantial portion of the entire channel (as by fallen trees), and in which individual sediment grains do not constitute significant form elements on the bed (as in step-pool torrents). The second condition requires that relative roughness, D/d (the ratio of particle diameter to flow depth), be less than 0.3 — usually it is much less. The transition to large channels, on these criteria, falls somewhere near bankfull discharge, $Q \approx 20\ \mathrm{m^3\ s^{-1}}$ and channel width, $W \approx 20$ m. Our examples, however, are drawn from experience of much larger rivers.

Morphological Classification

Rivers are one of the most active agents in shaping the surface of the earth and it is therefore not surprising that the earliest attempts at scientific river classification appear in the geological literature: W.M. Davis' (1899) classification of rivers by stage in an idealized erosional cycle as "youthful", "mature" and "old" probably remains the best known. It is based on an artificial concept of landscape evolution which begins with the relatively fast uplift of a land mass, followed by erosion at gradually declining rates until, at "old age", the land mass is worn down to an undulating plain of such gentle slope that little further erosion occurs. One reason why Davis' system has proven to be of little practical value is the fact that the recent geologic past (some 10^6 years) has been characterized by numerous ice age cycles, the most recent one ending only some 10 000 to 12 000 yr ago, barely an instant in geological terms. Fluvial landscapes in glaciated areas are rarely more than 12 000 yr old, but even in the rest of the world the rapid climatic and sea level changes associated with the glacial cycles initiated major adjustments in practically all river systems. It seems probable that today's rivers are more disturbed by outside forces (sea level change, climatic change) and are therefore more active and less uniform in appearance than the rivers of most geologic ages.

A useful geological concept (Schumm 1977) is to divide a watershed with its river system into three zones: Zone 1 — the drainage basins and headwater streams, as the source of water and sediment, Zone 2 — a conveyance zone in which water and sediment are transported by mainstem rivers with little loss or gain and Zone 3 — a deposition zone which may refer to fans, deltas or estuaries. The present study deals mainly with the conveyance and deposition zones, but events and land management in Zone 1 are often the key to understanding processes and morphology in Zones 2 and 3.

Rivers can also be viewed as the higher order links in the stream network of a drainage basin (Strahler 1952). Assuming one has a detailed map of a stream system, including all permanent or intermittent streams, order is defined as follows: first-order streams are the links between stream sources and the first confluence. When 2 first-order channels join they form a second-order link. In general where two streams of equal order join, they form a segment of the next higher order. Since stream order depends greatly on the scale of the maps used in determining it (Dunne and Leopold 1978, p. 499) and since stream networks are often controlled by geologic structure and rarely have a regular, tree-like appearance, stream order is not a reliable indicator of river size. Drainage area or some characteristic discharge are far more meaningful. However, most "large" rivers are at least of order 6, as determined on 1:50 000 maps.

There are so many aspects to fluvial morphology that a wide variety of river classification schemes is possible. Classification can be undertaken on the basis of quantitative factors, such as width-depth ratio, bed material size or channel slope, and qualitative factors such as channel pattern in plan or degree of confinement. A comprehensive review of literature on river classification is beyond the scope of this paper, but some typical approaches are discussed by way of examples.

The classification system of Kellerhals et al. (1976) provides an appropriate framework for this discussion, since its main objective is to recognize the many factors that make up a fluvial landscape and to describe them in a systematic manner, proceeding from a broad look at the setting of the river reach to the details of the channel cross section and profile. A secondary objective is the introduction of a consistent terminology.

The most important aspect of the physiographic setting of a river reach is the degree to which the river is affected by geologic constraints. Most rivers flow in valleys that exert some degree of lateral or vertical control over the river. Exceptions are rivers on deltas, fans or broad plains. Deltas are river-deposited surfaces built out into a body of water. Fans are alluvial, fan-shaped surfaces deposited where a narrow valley emerges onto a broad surface. Broad plains are likely to be either alluvial, lacustrine (beds of drained lakes), or emergent coastal plains.

Where there is a valley there can be widely different degrees of interaction between the valley and the stream, depending on the degree to which a river is associated with alluvial deposits and fluvial features such as terraces and flood plains. In the engineering literature the term "flood plain" is often qualified with a specific return period of "*n* years" to refer to any surface subject to flooding at least once every n years on a long-term average, without any genetic implication. In the geological literature and in the present paper the term "flood plain", sometimes qualified as "genetic", is restricted to surfaces built or deposited by the present-day river in the course of lateral shifting or flooding. Alluvial terraces are similar surfaces built some time ago by a river flowing at a higher elevation. The distinction between alluvial terraces and flood plains is not always clear, particularly in cases where there may be several, distinct alluvial surfaces associated with a river, all subject to flooding at different frequencies. In the fisheries literature the term "flood plain" generally refers to seasonally flooded areas associated with a river, including any shallow, permanent lakes in flood plain depressions or along the edges of the flood plain (Welcomme 1985). Many large rivers, particularly tropical ones, are associated with extensive systems of shallow lakes whose water levels are more or less closely controlled by river stage. Such lakes may form in the drowned mouths of tributary valleys if the mainstream river aggrades more quickly than the tributary can follow, or they may simply be low areas of genetic flood plain, located relatively far from the main channel and therefore receiving little or no sediment. Eventually such areas are left behind in the general slow process of flood plain aggradation and become seasonal or permanent lakes. On the very long term (10^3 to 10^4 years) one can expect the river to shift through such lakes and fill them up, but this will tend to elevate the river above flood plain areas elsewhere, forming new lakes in the process.

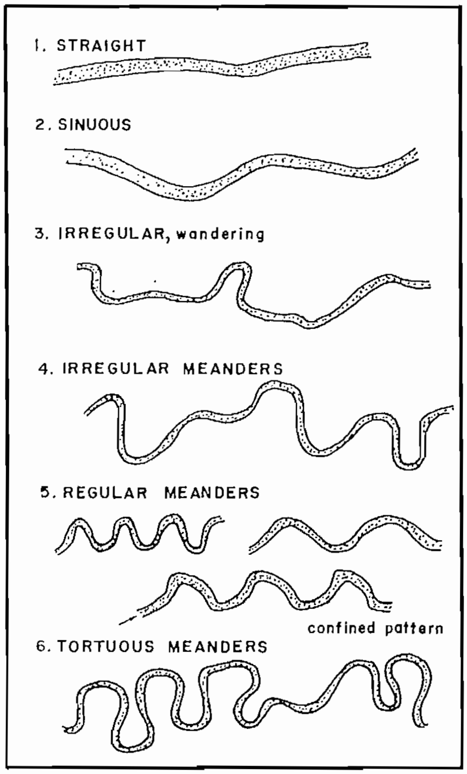
Almost all flood plains of the fisheries literature are genetic flood plains in the geologic sense of the term, but there are many other genetic flood plains that flood only infrequently, possibly only once in 10 yr on average and then only for a few days so that they are of less interest from a fisheries point of view.

Rivers in valleys without genetic flood plains are called incised or entrenched, canyons being an extreme case of incision. Rivers with at least some genetic flood plain may be confined to various degrees, depending on how severely their lateral development is restricted by terraces or other features of the valley walls. The degree of lateral interaction between a valley and its river is readily observable on air photographs.

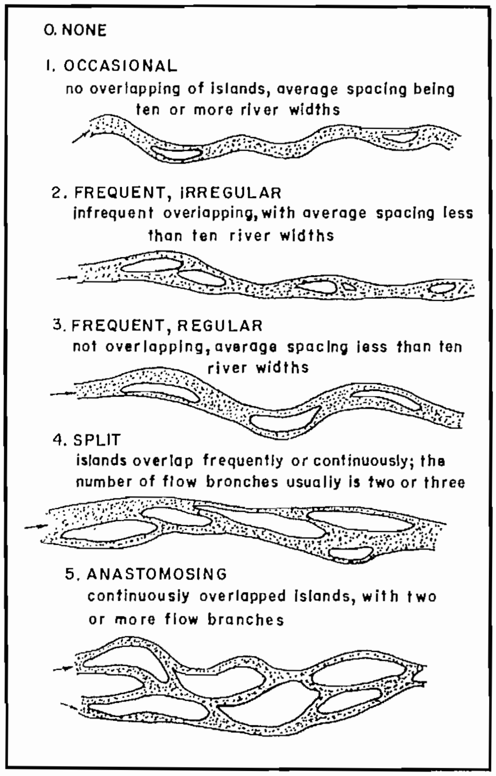
The degree to which a valley and its local geology exert vertical control over a river is also important and much more difficult to determine, depending primarily on the degree to which the river flows on self-transported and self-deposited materials (i.e. its own alluvium). Rapids over bedrock sills or over accumulations of course lag boulders are easily identified and are clear indications of external vertical controls, but the common situations where there are only occasional occurrences of non-alluvial and not necessarily very resistant materials on the river bed are far more difficult to identify. In situations where the alluvial deposits on a valley floor are not significantly deeper than the deepest scour holes in the river channel, one should assume that the valley floor slope exerts significant control over the river channel slope.

The plan form of river channels and channel bars is one aspect of fluvial morphology that has received much attention because of the great natural diversity and because proper interpretation can reveal a great deal about ongoing river processes. Particularly in cases where there are significant areas of genetic flood plain, one normally is justified in assuming that the appearance of the channel and flood plain reflect presently active processes. Figure 1 (A—D) illustrates the classification scheme and terminology of Kellerhals et al. (1976). The first two diagrams refer to the channel network in plan and address the two aspects of alignment and degree of anastamosing about channel islands. In split or anastamosing networks all channels need not necessarily have the same pattern. Channel islands normally are well vegetated surfaces reaching to at least flood plain elevation. Lower, unvegetated or lightly vegetated surfaces are channel bars and are addressed by the third diagram. Most channel bars are accumulations of channel bed materials. Their shape and rate of deformation or movement often allow approximate, quantitative deductions on bed material type (sand or gravel) and rate of transport.

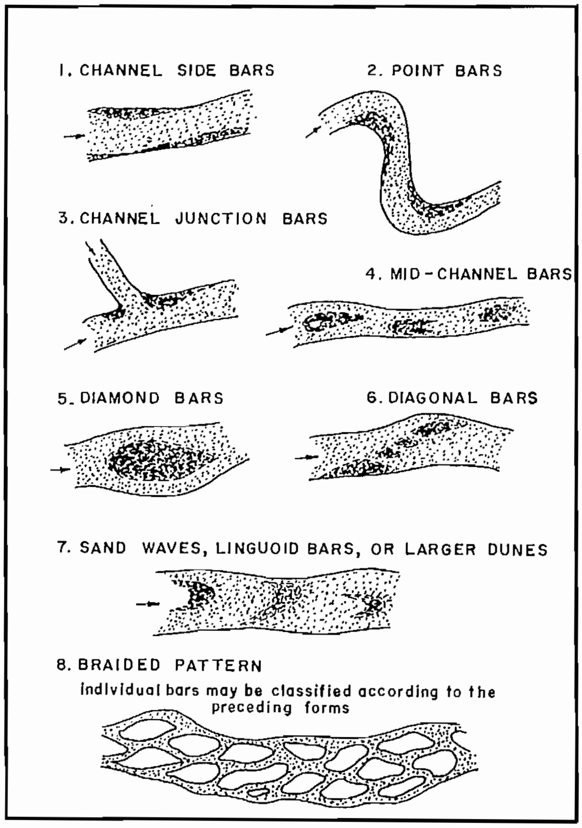
The last diagram deals mainly with the appearance of the flood plain from a geomorphologic point of view. Since most flood plains consist of channel bed materials overlain by deposits of suspended sediments, the appearance of the surface permits conclusions to be drawn on the relative mix of bed load and suspended load in the total sediment load. Flood plains also show former channel positions and permit conclusions on the rate and direction of lateral channel migration and on the processes responsible for channel shifting.



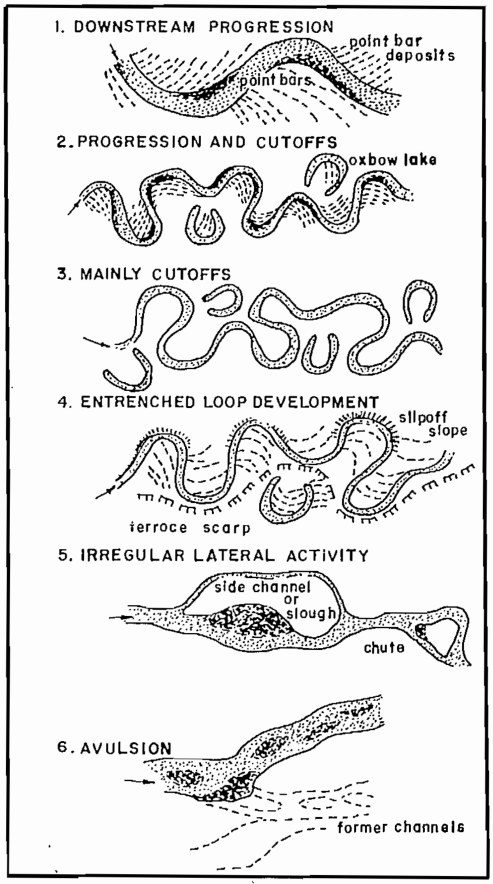
(A) CHANNEL PATTERN



(B) CHANNEL ISLANDS



(C) BARS



(D) LATERAL ACTIVITY

FIG. 1. Classification of planform features of river channels. Modified after Kellerhals et al. (1976).

In areas of sediment accumulation such as large flood plain systems or fans and deltas (Zone 3 of Schumm's geological classification) channels become subject to avulsion, because the channel and nearby flood plain areas tend to rise gradually above the elevation of distant, old parts of the deposition surface. Much of the sediment in the water spilling over a flood plain tends to deposit soon after it leaves the main channel, thereby building up the natural levees seen on many flood plains. Eventually, a large flood can lead to a rapid shift to an entirely new river channel, possibly many kilometres from the old one.

From a fisheries point of view the following aspects of flood plains are of particular interest:

—extent, duration and depth of seasonal flooding and the year-to-year variability of these parameters

—extent and depth of permanent flood plain lakes under wet, normal and dry conditions

—some measure of the degree to which flood plain lakes are connected with the main river channel and the duration of any periods when flood plain lakes are isolated.

All three items require information on land and water levels which cannot be extracted from a single set of air photos. Ideally, one will need a good understanding of the river's hydrologic regime and several typical flood plain cross sections. Sequential air photo coverage showing the state of the flood plain from maximum to minimum seasonal inundation will provide most of the information, particularly if a few water levels are also available.

Not all the river types conceivable on the basis of Fig. 1 do, in fact, occur, and there have been several attempts to reduce the multi-dimensional aspect of river plan form to one-dimensional classifications that would permit ready qualitative deductions on active river processes. The classification by Mollard (1973) is a well known example, illustrated here in Fig. 2. The system is based primarily on work done on the Canadian Northern Great Plains, but it has broad applicability, especially for air photo interpretation of flood plain deposits. Schumm (1985) has also presented a simplified form of this classification. Another, similar approach applicable to alluvial rivers, developed as part of an air photo study on river channel stability as related to bridge hydraulics, is illustrated in Fig. 3 (Brice 1982). Analyses by Savat (1975) and Holz et al. (1979) of the morphology of the largest tropical rivers indicate that the system of morphological characteristics presented here will satisfactorily describe rivers anywhere, although there may be regional variability in the occurrence of some features.

While river bars are channel features with plan dimensions comparable to channel width and are therefore best classified together with the appearance of the channel in plan, bed forms are smaller features with dimensions comparable to water depth. Figure 4 is a widely accepted bed form classification applicable to sand-bed rivers. Gravel-bed rivers do not normally have comparable bed forms, although dune-like features have been reported from very active, large gravel bed channels (Galay 1967). Bed forms are not only smaller than bars, they are also less persistent. During the passage of a flood wave, some sand bed channels can pass from dunes to a flat bed and on to antidunes, reverting back to dunes once flows have subsided.

Other aspects of fluvial morphology that do not require nominal classification systems because they are readily measured or described are: bed and bank materials, bank and flood plain vegetation, the discharge regime in the form

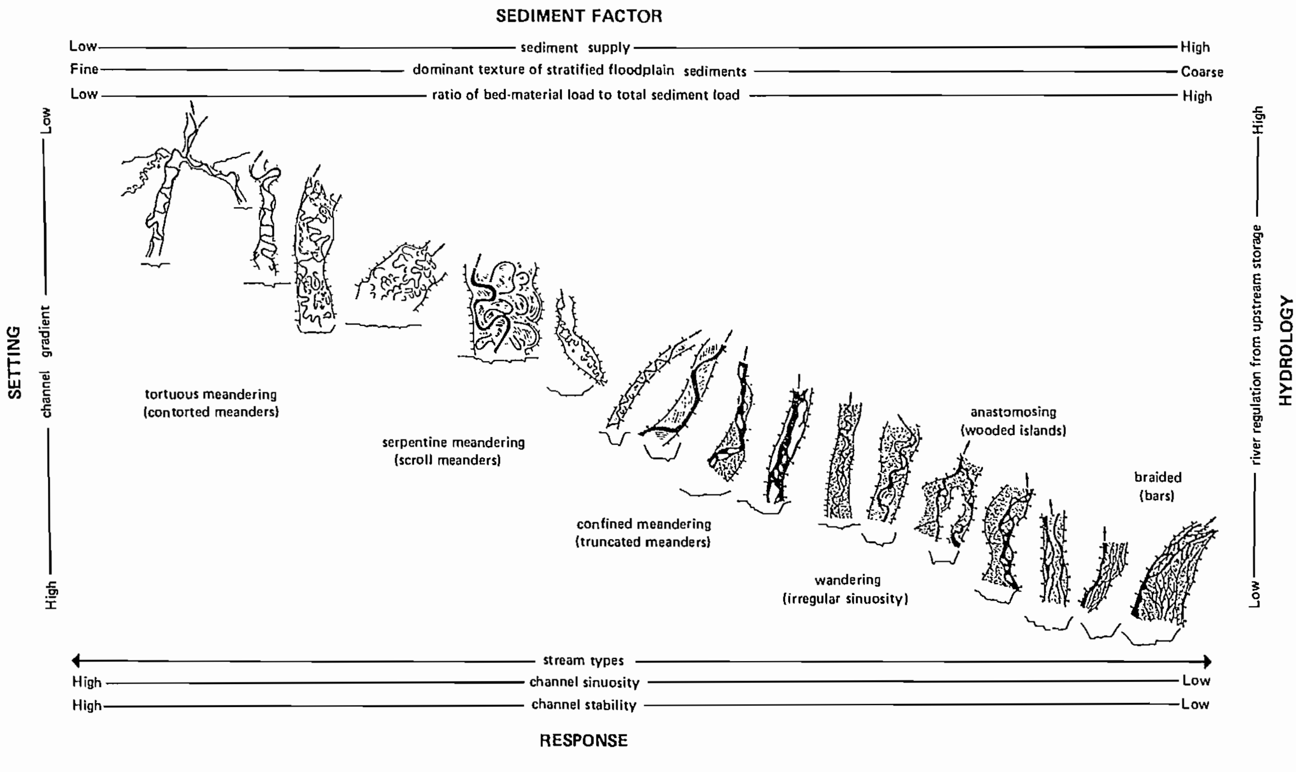


FIG. 2. Continuum of stream channel and floodplain types (modified after Mollard 1973). The top and side margins give generalized governing factors: the bottom of the diagram enumerates some principal response features.

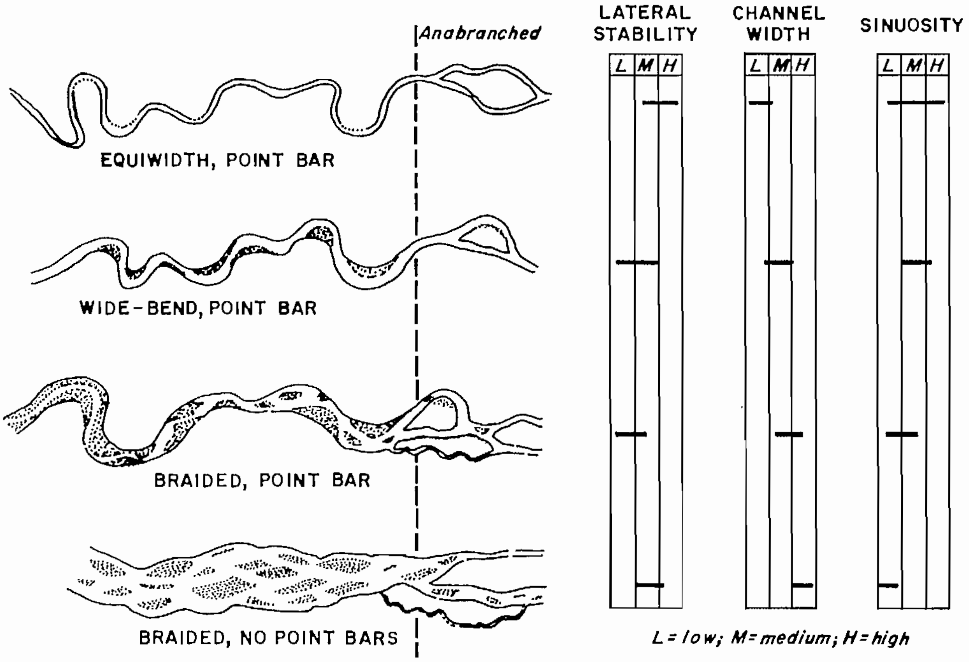


FIG. 3. Four basic channel types (Brice 1982). The classification is two dimensional insofar as each of the four basic types may occur in both single and multiple (anabranched) channel modes.

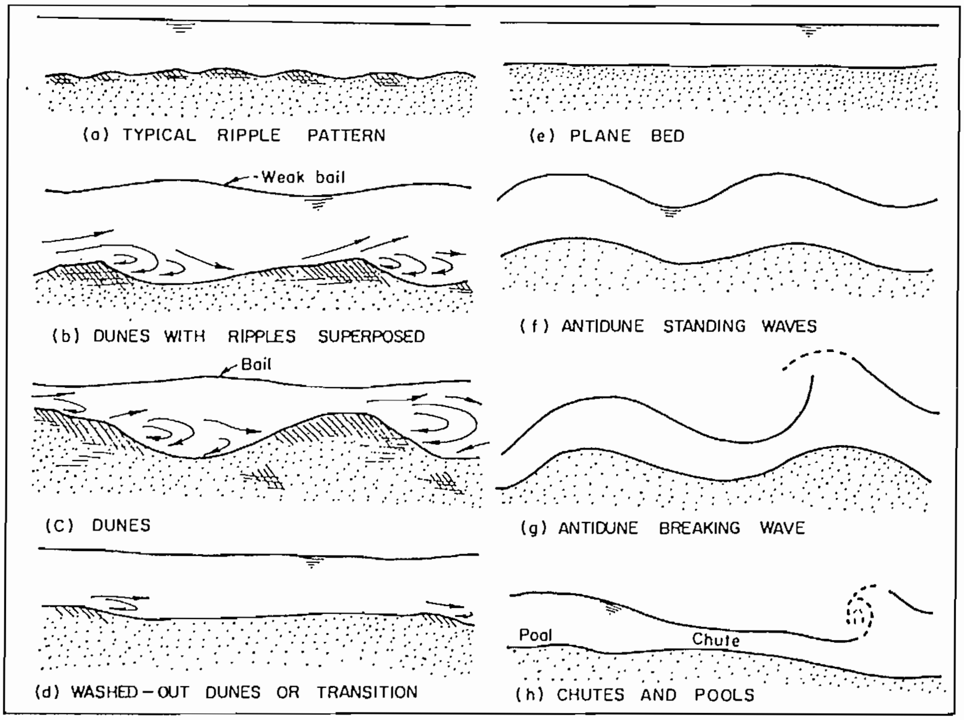


FIG. 4. Classification of primary bedforms in sand bed channels (Simons et al. 1965).

of a statistical description of the flow spectrum, the sediment transport regime in similar form, hydraulic geometry (e.g. width, depth, velocity, and slope over the entire range of normal flows), vertical and lateral channel stability (e.g. aggradation or degradation rates, bank erosion rates) and, in northern rivers, information on the ice regime such as location, frequency and height of ice jam flooding.

Some of these parameters are not easily obtained and, depending on circumstances, many may not be relevant, but they do form part of a full morphological description. Many investigators have attempted to correlate one or more of these parameters with channel pattern, so that they may be inferred in reconnaissance studies. Discussion of methods for the systematic determination of morphologic parameters either by means of interpreting maps and air photos, or through field surveys, is beyond the scope of this paper. Neill and Galay (1967) describe a general approach to river surveys. Checklists for air photo interpretation are given in Kellerhals et al. (1976). A very detailed description of the US Army Corps of Engineers river survey procedures is given in Thomas (1977).

Factors Determining Morphology

The ideal alluvial river is formed in situations where a stream emerges from an upland area into a large geological depression (e.g. old lake basin) with an outlet at a fixed elevation. Similar conditions can be created in laboratories by feeding a water and sediment mixture into a large box, a so-called river tray, with a fixed outlet. In such situations a stable equilibrium will eventually be reached when net deposition ceases. At this stage, the depression will have been infilled and converted to an alluvial plain with a river flowing across it. The morphology of that channel and flood plain will depend almost entirely on the discharge and sediment supplied from upstream. Laboratory studies have shown that, although no two experimental rivers will be identical, the results are consistently reproduceable in a statistical sense.

In real rivers, vegetation and land use on the flood plain must be expected to have secondary effects. Vegetation does affect the erosion resistance of river banks, and therefore the lateral channel shift rate, but effects on the dimensions of large rivers appear to be small (cf. Hickin 1984; Nanson and Hickin 1986). As illustrated in Fig. 5, the width of large rivers ($Q > 20$ m^3 s^{-1}) from various parts of the world is remarkably consistent. Land use can entail any degree of interference with a river ranging from some clearing on the flood plain to complete channelization between dikes. Clearing is unlikely to have major effects on the channel dimensions of a large river, but tends to lead to accelerated channel shift rates.

Local climate is generally also a secondary effect, but it can be important, for example, in very cold climates where the formation of ice-rich permafrost under the flood plain leads to a peculiar set of bank erosion processes (Church and Miles 1982). River ice and the associated ice jamming at freeze-up and break-up affect flood levels and therefore the height of flood plains (cf. Kellerhals and Church 1980). In very dry climates water losses into the ground may become significant and can result in rivers that shrink in size or even disappear.

Ideal alluvial rivers as described here are rare, but many situations approach the ideal state. Examples are alluvial river reaches some distance above their deltas, where the effects of delta progradation and sea level changes can be neglected, as in some of the rivers on the Indo-Gangetic plain. Rivers on slowly growing fans and deltas may also closely approach the ideal situation.

The vast majority of the world's rivers are not flowing on truly self-deposited surfaces, but rather across surfaces or in valleys that pre-date the present-day river or have at least been significantly affected by non-fluvial processes such as tectonic uplift or tilting, glacial scour or infill, sea level changes and catastrophic events like landslides. The basic difference between such rivers and truly alluvial rivers

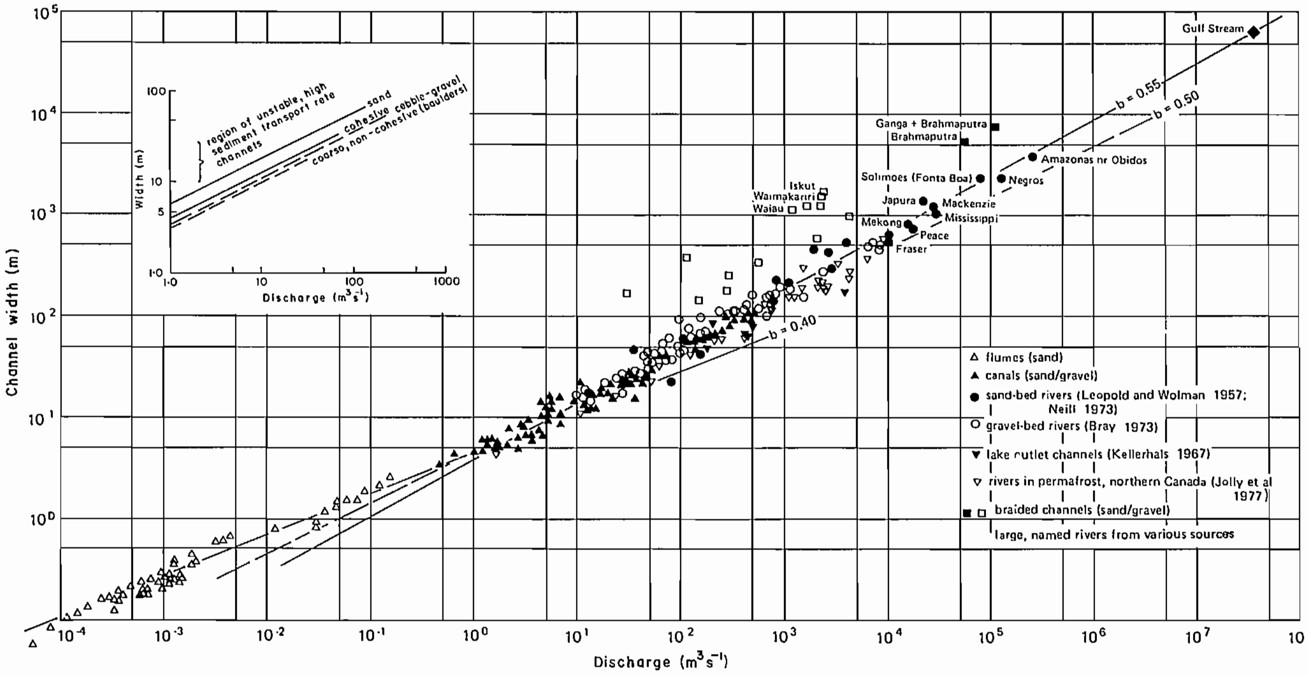


FIG. 5. Scale relation for channel width vs. flow. Small straight channels have $w \propto Q^{0.4}$ indicating that dynamical similarity is maintained. However, large river channels have $w \propto Q^{0.55}$, approximately, indicating that they become distorted to relatively greater width as they grow larger. Inset: variation in channel width at a given discharge due to material, properties based on Simons and Albertson (1960).

is that the valley floor slope is not set by the river but rather imposed externally. Since the river may still have some lateral freedom and may therefore be able to adjust its channel slope by adopting a certain sinuosity, channel slope is neither fully imposed, nor fully self-formed. The basic reason why most rivers are not flowing on self-formed surfaces is the enormous length of time needed to develop a self-formed surface because of the vast amount of sediment that must be shifted. In the case of major rivers this might involve time periods of the order of 10^5 years, during which time there would have to be relatively little tectonic disturbance or sea level change. Some of the world's biggest rivers do meet this criterion (Potter 1978), but they represent exceptions, not the general rule.

In practical terms this means that although channel slope is theoretically a morphological parameter largely determined by the water and sediment supply to a river reach from upstream, it nevertheless has to be accepted as an imposed parameter, except in special situations where the reach of interest may be very short, channel materials very easily moved or the time frame unusually long.

Similar arguments concerning dependence or independence of parameters apply to other morphological variables, depending on the time scale of interest. Channel width of large rivers, for instance, is clearly a dependent scale parameter on a geological time scale, determined principally by water and sediment supply from upstream. This applies even in bedrock canyons. If the upstream supply is changed by the action of man, such as through irrigation diversions out of river system, width might have to be treated as dependent or independent, depending on the time frame of the investigation and on the ability of the river to change its width. Stable, well incised channel reaches of rivers with small sediment loads will clearly not be able to reduce their width quickly by sedimentation to adjust to a regime of reduced flows, although vegetation might encroach into the formerly unvegetated channel zone. Project assessments would have to accept the existing channel width as imposed or fixed. In relatively unstable channels with large suspended sediment loads, on the other hand, width adjustments can take place in a matter of years and would clearly be of major significance in any assessment of the morphological effects of a proposed diversion.

Within very short time frames of weeks to months, most morphological parameters become invariant and the river channel can be assumed to act essentially as an inerodible conveyance channel for water and sediment. Standard hydraulic conveyance formulas (e.g. Manning's equation), which permit the estimation of depth and velocity for given channel dimensions, channel roughness and discharge are applicable without reservation only under such conditions of stable morphology. All sediment transport formulas are similarly restricted. Many stable river reaches, particularly incised, non-alluvial or partially alluvial reaches maintain their morphology over centuries, but in the case of truly alluvial reaches and particularly those affected by recent man-made interferences, assumption of an invariant morphology is rarely justified. Another important exception occurs in alluvial sand-bed channels, many of which scour and fill significantly through a flood event.

The discharge regime supplied to a river reach from upstream is clearly the most important factor determining river morphology and there have been numerous studies carried out to quantify this relationship. The problem of designing stable, unlined irrigation canals on large alluvial plains in British India provided the impetus for some of the earliest work (Lacey 1930; Blench 1969). Both stable river and stable canal dimensions were found empirically to vary with discharge approximately as follows:

(1) $w = a_1\ Q^{b_1}$

(2) $d = a_2\ Qs^{b_2}$

in which w is channel width, d is mean depth, Q is the bankfull discharge in the case of rivers or the design discharge for irrigation canals. The exponents b_1 and b_2 were estimated as 0.50 (see Fig. 5) and 0.33 respectively, and the coefficients a_1 and a_2 were assumed to be constant, at least for any particular river system and the canals distributing its water and sediment.

After an extensive study of data from stream gauging sites, primarily in the midwestern USA, Leopold and Maddock (1953) came to remarkably similar results, although their best estimate of b_2 was 0.4. They used mean annual flow as the independent variable, but they also showed that the exponents b_1 and b_2 remain remarkably constant for any consistently applied discharge estimates (Fig. 5). Simons and Albertson (1960) examined a diverse set of irrigation canal data which confirms the basic functional form (value of b) of Equations 1 and 2 and provides estimates for the coefficients a_1 and a_2 for various bed and bank conditions. The insert of Fig. 5 is derived from their results and shows width-discharge relations for canals in various uniform materials.

The above pioneering work has been followed up by a large number of studies dealing with the "hydraulic geometry" of rivers in widely different settings. Kellerhals (1967) analyzed lake outlet channels on gravel beds, a data set for which it was possible to assume that there was no sediment supply from upstream. Bray (1973) and Neill (1973) analyzed a large set of river data from Alberta, Canada. Bray, looking at gravel bed channels, found that a consistently defined discharge such as bankfull flow or the 2-yr flood is the only independent variable that contributes significantly towards explaining the width and depth of the various river channels, however both bed material size and discharge contribute towards explaining the variation in channel slope. Neill, on the other hand, in looking at the sand bed channels found that a morphological classification based on channel plan form helps explain width and depth variation in a minor way, and contributes significantly towards explaining slope variation. This is quite consistent with the notion that slope may be externally imposed on many rivers and that they adjust to it by adopting different channel patterns in plan.

We have collected data from braided channels, channels that clearly have a large upstream sediment supply. Figure 6, a slope-discharge plot of the data, shows scatter over at least one logarithmic cycle. Many factors probably contribute to this, but the quantity and size distribution of the upstream sediment supply is likely the most important one.

The effect of upstream sediment supply on river morphology is far more difficult to quantify than the effects of discharge, because of lack of data and diversity of effects. Rivers transport sediment both in suspension, the suspended load, and by rolling, sliding and bouncing ("saltating") along the bed, the so-called bed load. In terms of volume, the suspended load is normally from 1 to 2 orders of magnitude greater than the bed load; it is also far more easily mea-

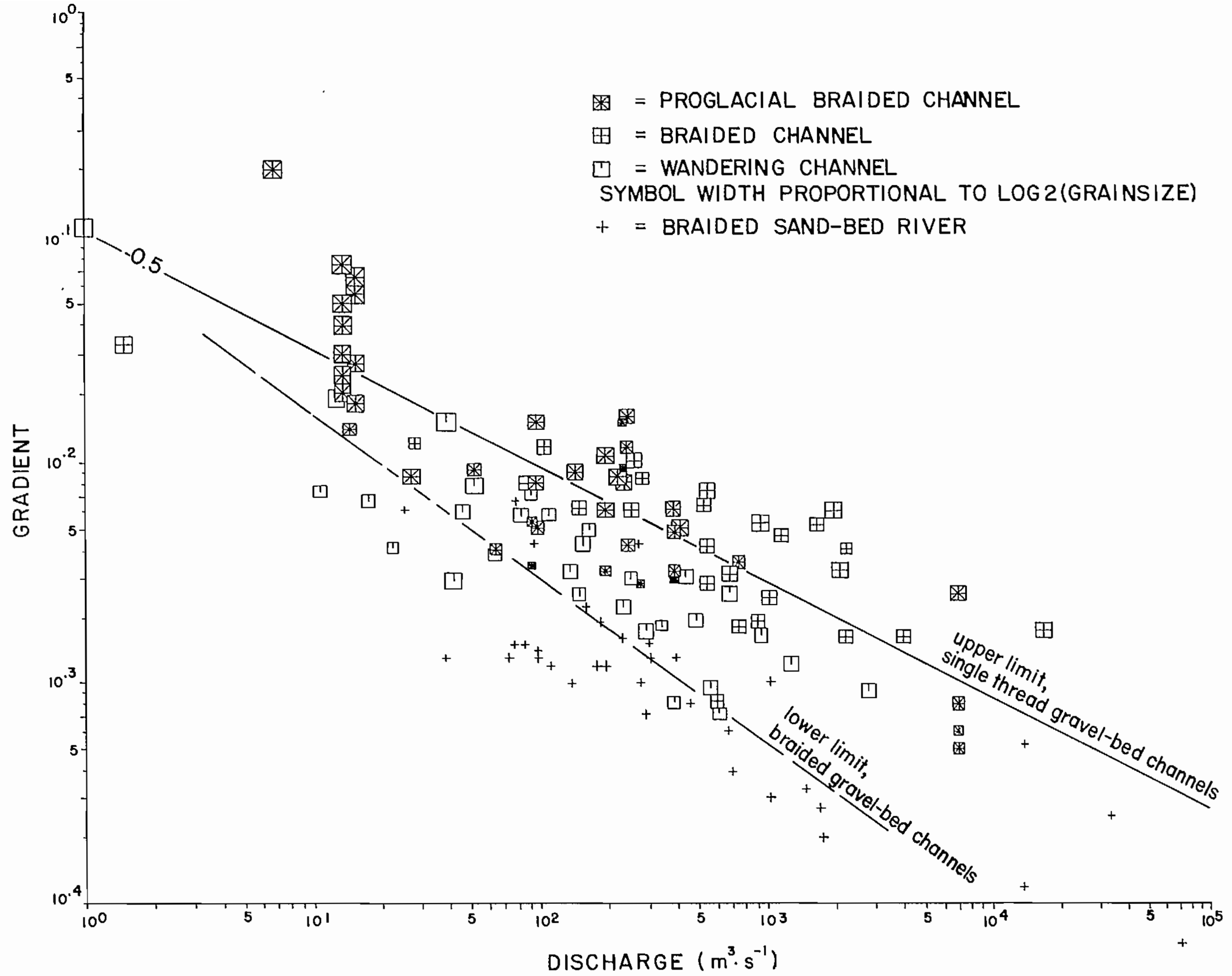


FIG. 6. Channel gradient vs. discharge in braided channels and non-braided gravel bed channels. The upper line gives an upper gradient limit for non-braided channels: the lower line delimits the lower limit of braided gravel channels. Sand-bed channels continue to braid on lower gradients. Both gravel criteria exceed the well-known discriminant function of Leopold and Wolman (1957).

sured. The bed load on the other hand involves the materials that form the channel bed and bars and is therefore of prime interest when considering channel morphology. It is very difficult to measure.

The foregoing defines fluvial sediment according to its mode of transport. It is often morphologically more relevant to split it into bed material load — the load fraction that occurs in significant quantities in the local channel bed, and wash load — the load that is finer than the local channel bed materials. The rate of bed material transport is related to local hydraulic conditions and there are many formulas available for its estimation, although there is no consensus on which is best and the results can be expected to differ by orders of magnitude (Vanoni 1975, p. 221). The rate of wash load transport is determined purely by upstream supply. In most gravel bed rivers the bed load of coarse sand and gravel is essentially identical to the bed material load, while the suspended load of clay to medium sand corresponds to the wash load (i.e., Fraser River at Agassiz, described in McLean and Church 1986). In sand bed rivers, however, both the bed load and a major part of the suspended load may be part of the bed material (i.e., Orinoco River at Musinacio, described in Meade et al. 1983), while in cobble and boulder channels the gravel-sized particles in the bed load might be a wash load component.

Channel stability has long been known to be a qualitative measure of bed material transport rate. The highest gravel transport rates are associated with braided, wide, shallow and very unstable proglacial rivers (Fahnestock 1963) while the slightly incised, very stable gravel bed rivers of Alberta move their bed materials only infrequently and carry small loads. Mollard's channel pattern classification of Fig. 2 expresses this relationship. Neill (1987) has been remarkably successful in relating a quantitative measure of channel instability, the lateral channel shift rate, to measured bed material transport rates.

The suspended load primarily affects channel shape because it is deposited nearbank, overbank during floods and so determines streambank composition. Schumm (1977) noted that rivers in the midwestern USA increase in width below tributaries carrying relatively large loads of coarse, noncohesive bed material (sand and gravel), while width decreases below tributaries supplying large suspended load of silt and clay. This is consistent with the findings of Simons and Albertson (1960) for canals.

Flood plain deposits reflect the composition of the suspended load. With silt and clay being far more erosion resistant than sand, silty–clayey flood plains resist the development of cut-offs more effectively than sandy flood plains and can therefore evolve tortuous meander patterns of high sinuosity.

Geophysical Basis of Riverine Habitat

Equations (1) and (2) form a closed set if combined with the equation defining discharge,

(3) $Q = wd\bar{v}$

where $\bar{v}$ is mean velocity of flow. By algebraic manipulation, we find that

(4) $\bar{v} = (1/a_1a_2)\ Q^{1-(b_1+b_2)}$

Further,

(5) $A = a_1a_2\ Q^{(b_1+b_2)}$

where A is cross-sectional area of flow. Although these equations were developed to describe the variation in channel size and form between different rivers or along a particular river but at some characteristic fixed discharge such as the local 2-yr flood, as discussed in the last section, they can also be applied to a single site (i.e., a short channel length within a single reach) to describe the changes in flow geometry as discharge varies in the short term within the essentially fixed channel (cf. Fig. 7). Such a description is called hydraulic geometry at-a-station, to distinguish it from the above so-called downstream hydraulic geometry (Leopold and Maddock 1953). In this at-a-station context, the equations aid habitat description.

The storage-discharge equation (5) describes water volume per unit length of channel (or total volume for the length of channel over which A is averaged) as flow varies. Similarly, the velocity equation (4) gives mean flow velocity in the reach, and the width equation (1) closely approximates the area of bottom per unit length of channel. Figure 7 illustrates these functions for two gauged reaches in Fraser

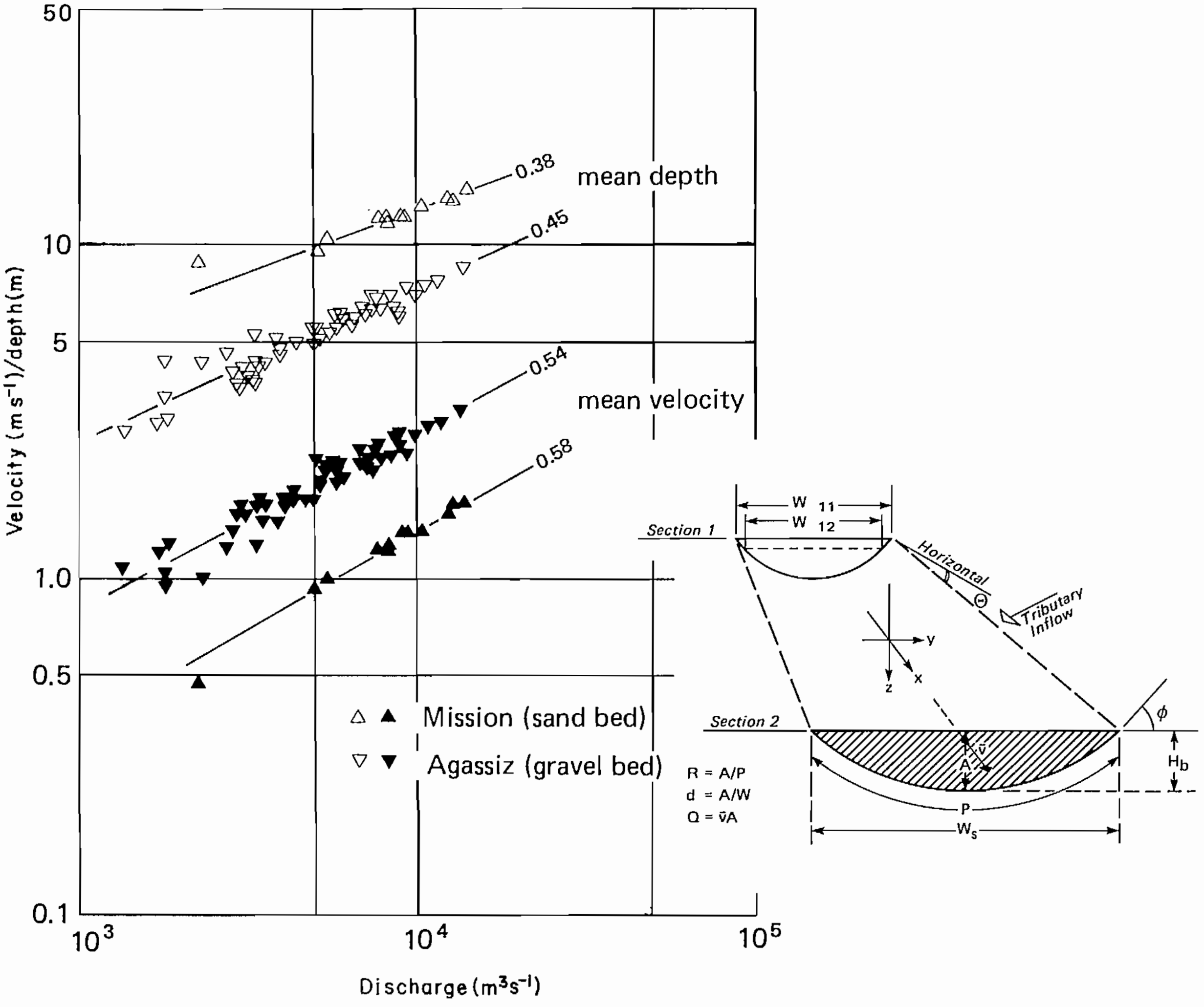


FIG. 7. Hydraulic geometry at a station on Fraser River, British Columbia, in gravel bed (D_{50} = 25 mm) and sand bed (D_{50} = 0.38 mm) reaches. *Inset*: definition diagram for reach averaged hydraulic geometry.

River, British Columbia. In this at-a-station application, the parameters a_i and b_i depend upon bed and bank material characteristics (Knighton 1974) and may vary widely.

In fact, habitat characterization usually requires more refined assessment of depth and velocity distributions. Figure 8a illustrates the distribution of depths as flow varies on Fraser River at Mission. In this rather regular trapezoidal section (the banks are rip-rapped at the angle of repose), the area with shallow flow and light penetration to the bottom is very restricted (Fig. 8b). Figure 9 compares an idealized trapezoidal section (typical of straight channels) and a triangular section (typical of bends). The latter provides a much larger area of shallow water, and more varied range of depth and velocity at all flows. Channelization tends to promote the former set of conditions.

A similar diagram can be developed for velocity distribu-

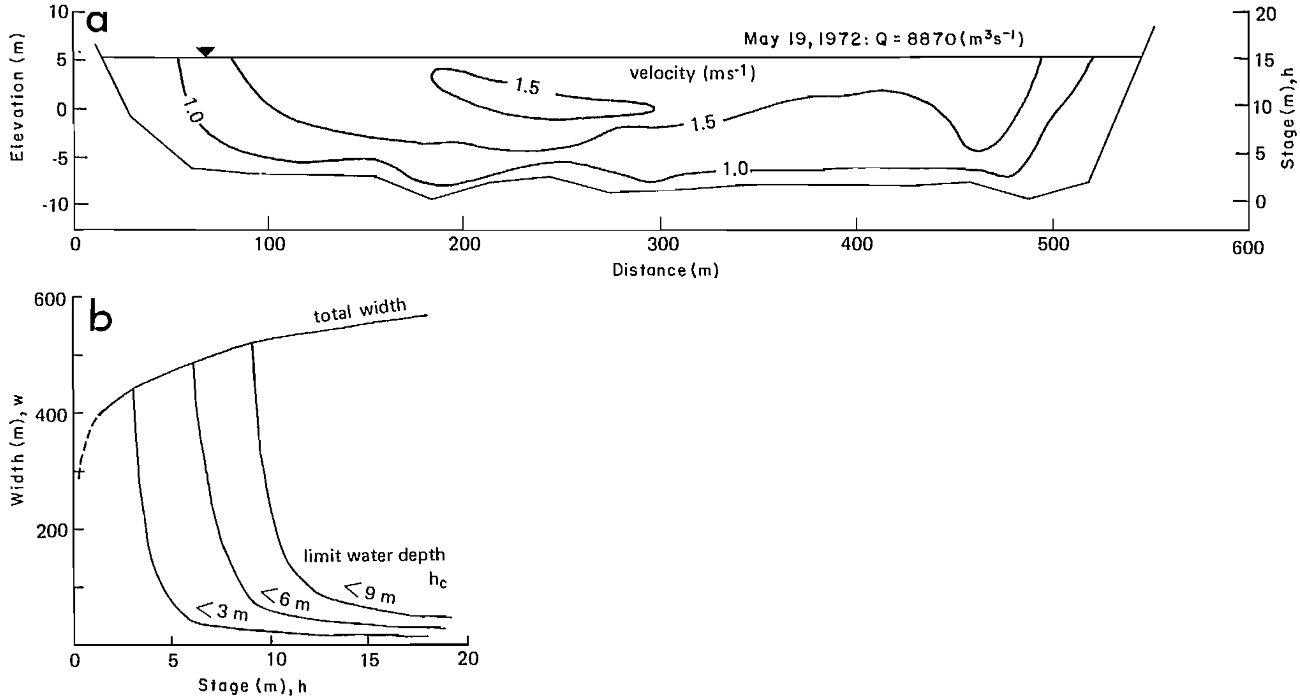


FIG. 8. Variation of bed area with various limit water depths on Fraser River at Mission, British Columbia: (a) Cross section of the river, showing velocity distribution. (b) Depth-area plot of the channel.

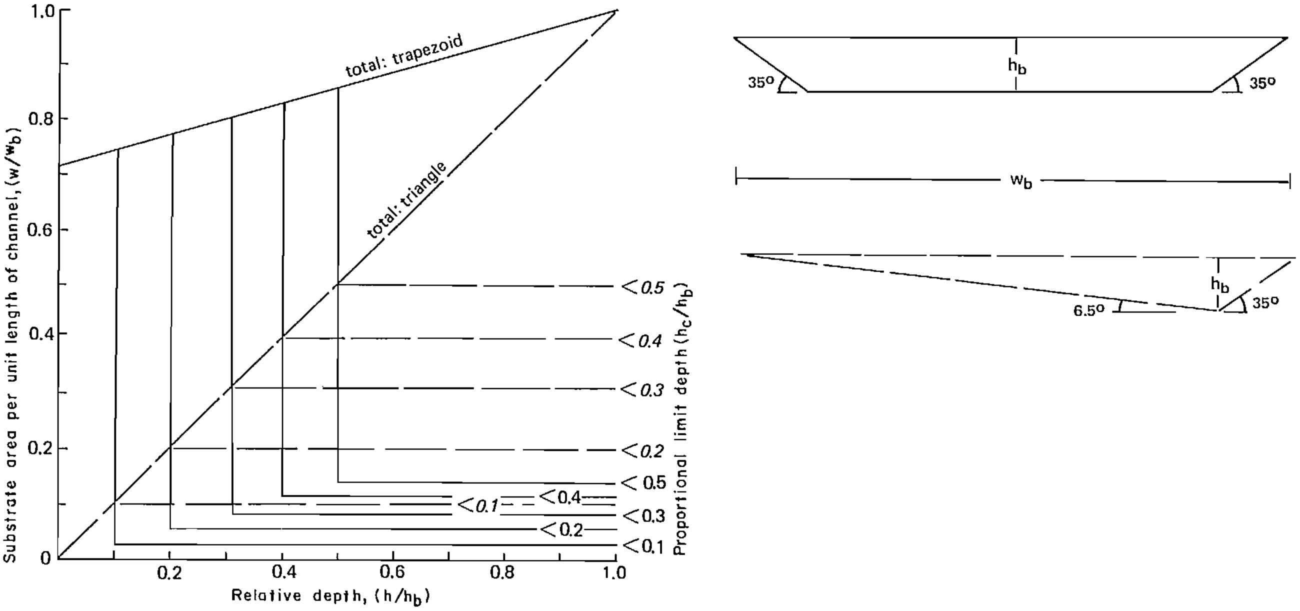


FIG. 9. Depth-area plots for ideal trapezoidal and scalene triangle sections (plots are non-dimensional).

tion, or for near bed velocities or joint depth–velocity distributions, but these require field measurements over the range of flows and so the labour is great. As an alternative approach, simulation has been used. To be reasonable, hydraulic constraints discussed in the last section must be observed. This topic is taken up by Stalnaker et al. (1989).

As can be appreciated from Fig. 8a, habitat conditions vary substantially across a river. The centre of the main river channel often is a relatively barren or hostile environment, since high velocities or high sand transport rates maintain a sterile substrate and exact a large energy toll from fish to maintain themselves there. The channel side is often more favourable hydraulically and as a food supply area. In large rivers the secondary channels of anastomosed or braided reaches often provide the best habitat. Relatively little study has been given to the comparative morphology of these sub-channels. Anabranches in anastomosed systems often are taken to be regime equivalents (in the downstream sense) of the main channel. Data of Anderson and McKay (1973) for Mackenzie delta distributary channels (which debouche into the microtidal Beaufort Sea), and of Galay et al. (1983) for the inland anastomosed upper Columbia River are consistent with the trend established in Fig. 5, which lends support to the hypothesis. Viewed locally, individual channels may depart from the regime type of the main channel if sediment transport through the anabranches — hence bed and bank materials — departs systematically from that in the main channel. Because of sediment exclusion effects at anabranch entrances, this is entirely possible. Individual braid channels in sand appear to replicate the behaviour of major braided rivers (data of Church and Gilbert 1975), but the individual gravel braid channels observed by Fahnestock (1963) appear to be similar to single thread channels. Because of downstream effects associated with tidal prism storage, the hydraulic geometry of tidal entrances also appears to be systematically different than in most non-tidal rivers. Downstream increase in width (hence habitat area) of tidal entrances appears to increase as $b_1 \approx 0.7$ (Langbein 1963), whilst mean velocity barely changes at all.

Individual braid channels do not remain stable for long, but anastomosed systems — particularly if their banks are heavily protected by riparian vegetation, as is prevalent in the humid tropics — may present highly stable habitat units.

Morphological Changes

Although we do have a broad understanding of what determines river morphology, predicting morphological changes due to interference with the controlling factors remains difficult, mainly because of the many interacting processes.

Equations 1 and 2 provide quantitative relations between discharge and channel size and they can be used for prediction provided that no other significant parameters change and provided further that the river has the ability to make the predicted changes through erosion or deposition within the time frame of interest. Unfortunately, these conditions rarely apply. Except at lake outlets, imposed discharge changes tend to be associated with equally imposed sediment load changes that will eventually affect bed and bank materials, thereby violating the assumptions underlying Equations 1 and 2. Since slope is also tied to discharge, any discharge change is likely to induce tendencies toward aggradation or degradation and that can have drastic effects on many other aspects of morphology, such as channel plan form or bed and bank materials.

Lane (1955) attempted to summarize the interdependencies amongst discharge Q, bed material load Q_{bm}, bed material size D and slope S in a purely qualitative manner as

(6) $Q_{bm}\mathrm{D} \propto QS$

The exact quantitative form of the equation is likely to depend on many other factors and remains unknown in general. Paris (1984) presents a resolution that assumes particular hydraulic and sediment transport functions.

Along similar lines Schumm (1977) has tried to estimate at least the direction of change in the main morphologic variables due to typical imposed changes. Flow regulation by a large storage dam, for example, typically reduces or eliminates the bed material load downstream ($Q_{bm}{}^{-}$) and reduces the morphologically important high flood flows (Q^{-}). The effect on morphologic parameters downstream are estimated by Schumm for this situation as

$Q^{-},\ Q_{bm}{}^{-} \rightarrow w^{-},\ d^{\pm},\ S^{\pm},\ F^{-},\ \lambda^{-},\ P^{+}$

in which F is the width–depth ratio w/d, λ is the meander wave length, and P stands for channel sinuosity.

Following Schumm's approach, we have considered the effects of changes imposed on the three variables discharge (Q), relative bed material load (q_{bm}) and relative wash load (q_w), both for single variables and for a few selected combinations (Table 1). The relative loads q_{bm} and q_w are defined here as Q_{bm}/Q and Q_w/Q, respectively. It is important to split the sediment load into its two components of bed material and wash load because they have different downstream effects. Relative sediment loads are used rather than absolute loads because most normal types of man-induced changes affect both discharge and sediment loadings and it is the relative change in downstream loading that leads to either sediment-deprived or sediment overload reaches. The reliability of the predictions in Table 1 varies greatly from well-established fact to essentially unsubstantiated judgements by us. Discussion of the evidence for each separate entry is far beyond the scope of this paper. The time scale of the changes in Table 1 is variable. While it may be as short as one year for median bed material size, D_{50}, and for the percentage silt and clay in the channel perimeter, M, it might take several centuries for changes in slope, S, and meander wave length, λ, to become clearly established.

The significance of the morphologic changes addressed by Table 1 is best illustrated on the basis of case histories. The following sections give brief summaries of some recent Canadian experience.

Interbasin Diversion

In the course of a hydroelectric project study, Kellerhals et al. (1979) assembled data on Canadian interbasin diversions. Diversions generally result in morphologic change along both the receiving (Q^{+}) and the depleted (Q^{-}) river. Relative bed material load and wash load changes can be in either direction and the direction can change at major tributary confluences; if the diversion scheme involves a dam on the depleted river, the direction of change immediately below the dam will be Q^{-}, $q_{bm}{}^{-}$, $q_w{}^{-}$, but below a heavily loaded tributary this can change to $q_{bm}{}^{+}$, and/or $q_w{}^{+}$.

The Kemano project of the Aluminum Company of

TABLE 1. Qualitative changes in major morphologic parameters for selected imposed changes.

Case	*Imposed changes*			*Probable direction of resulting change*								
No.	Q	q_{bm}	q_w	w	d	S	D_{50}	F	λ	P	M	Remarks
1	+	−	−	+	+	−	+	$-/\underline{+}$	+	+	−	Assuming no change in Q_{bm} and Q_w
2	−	+	+	−	−	+	−	−/+	−	−	+	
3		+		+	−	+	$\pm$	+	?	−	−	Change in D_{50} depends on type of material supplied from upstream.
4		−		−	+	?	+	−	?	+	+	
5			+	−	+	?	−	−	?	+	+	
6			−	+	−	?	+	+	?	−	−	
7	−	−	−	−	$\underline{\pm}$	−	$\pm$	$\pm$	−	+	−	Depends upon balance in Q, q_{bm}
8	−	−	+	−	−	−/+	−	$\pm$	−	?	+	
9	+	+	+	+	+	$\pm$	$\pm$	$\underline{\pm}$	+	?	$\pm$	
10	+	+	−	+	+	$\pm$	$\underline{\pm}$	+	+	−	−	

LEGEND:

Q Channel-forming discharge, approximately 2–10-yr flood
q_{bm} Relative bed material load, Q_{bm}/Q
q_w Relative washload, Q_w/Q
w Channel width
d Channel depth
S Channel slope
D_{50} Median bed material size
F Width/depth ratio
λ Meander wavelength
P Sinuosity
M Percent silt and clay in channel perimeter materials

NOTE:

All parameters are associated with discharge Q.
If initial changes are thought to be different from long-term changes they are separated by /. If change can occur in either direction it is shown as $\pm$, with the more probable direction emphasized as $\underline{+}$ or $\underline{\pm}$.
Imposed changes are assumed to be relatively large but not large enough to change the order of magnitude of the affected parameter.

Canada involves a large storage dam (Kenney Dam) without any outlet works on the Nechako River in British Columbia, a power diversion across the Coast Mountains to the Kemano River and a diversion of the spillway flows across a low divide to the Cheslatta River, which eventually flows back into the Nechako some 7 km below Kenney Dam. The dam was closed in 1954.

Between Kenney Dam and the Cheslatta confluence, Nechako flows are reduced to a trickle provided by dam seepage and small tributaries. Since the reach was a bedrock canyon and the local tributaries carry little sediment, morphologic change is exceedingly slow. Vegetation has encroached into the former channel zone and has attracted much activity by beavers, to the extent that the canyon is now a cascade of beaver dam controlled ponds.

Below the Cheslatta confluence, the Nechako River is significantly depleted (Q^-). In terms of the 10-yr flood, the depletion ranges from 28 percent at the Cheslatta confluence, to 20% some 281 km downstream, at the confluence with the Fraser River. In terms of mean annual flow, the depletion is 64% at the Cheslatta confluence, decreasing to 31% at the Fraser confluence. The river always was a lake outlet channel with negligible q_{bm} and q_w. q_{bm} remains negligible for the spillway flows routed through the Cheslatta valley because of a lake along that route. q_w has probably increased somewhat due to the massive erosion along the Cheslatta River. In the lower reaches of the Nechako, there is a definite increase in relative washload, q_w, since several tributaries carry significant wash loads and the diluting capacity of the Nechako is now reduced.

The pre-project morphology is documented only on air photos, but they show clearly that there has been remarkably little change after 30 yr of project operation. Most of the river length consists of a stable, incised, single channel. There is a narrow strip of newly encroaching vegetation along both banks. The tops of a few gravel bars are now vegetated and are gradually becoming channel islands. The gravel bed material shows no evidence of recent movement and there is some evidence of deposition of sand and fine gravel over formerly coarse gravel beds immediately below tributary confluences. The few unstable channel reaches show the most pronounced changes with extensive vegetation encroachment onto sand and gravel bars. Some back channels are vegetation choked and no longer flowing. The diretion of changes is shown in Table 2, using the notation of Table 1.

From a fisheries perspective, positive changes in F and M are important. The width–depth ratio has a direct bearing on water temperature, with increasing F indicating a greater tendency for river water temperature to follow air temperature. Increasing F also indicates a greater extent of shallow water, which may have positive or negative implications in terms of habitat. M is related to spawning gravel quality; increasing M values suggest decreasing quality.

The pre-project Cheslatta River was a small, lake outlet channel with a mean annual flow of order 1 $m^3 s^{-1}$, and a

TABLE 2. Direction of morphologic change for case studies.

	Imposed changes			*Direction of resulting change*							
River reach	Q	q_{bm}	q_w	w	d	S	D_{50}	F	λ	P	M
Nechako River, below Cheslatta confl.	−		+	−	−	n.c.	−	+	n.c.	n.c.	+
Cheslatta River											
upper reach	**+**	−	−	**+**	**+**	+	**+**	+	+	−	−
lower reach	**+**	−	+	**+**	**+**	−	+	+	+	−	−
Kemano River											
initial 20 years	+	−	−	+	+	+	n.c.	+	?	−	−
final, upper reach	+	−	−	±?	+	−?	+?	−	?	−	−
final, lower reach	+	+	−	+	+	n.c.	n.c.?	+	+	−	n.c.?
Peace River											
below dam	−	−	−	−	−	n.c.	n.c.	+	n.c.	n.c.	±?
above Pine R. confl.	−	−	−	−	−	−	−	−?	n.c.	n.e.	−
below Pine R. confl.	−	+	+	−	−	+	−	+	n.c.	n.c.	−

NOTES: ? indicates that the direction of change is either not known or not well documented. Heavy symbols, e.g. **+** indicate a drastic change.

2 yr flood of order 10 m^3 s^{-1}. From its source in Skins Lake, it followed a meandering course along 22 km of glacial spillway trench, then passed through Cheslatta Lake on to the Nechako River. Spillway flows from the Nechako reservoir to Skins Lake have generally been in the range of 50 m^3 s^{-1} to 180 m^3 s^{-1} for several months each year, but have reached as high as 538 m^3 s^{-1}. The mean annual spill is 73.5 m^3 s^{-1}. This is a classic case where the imposed discharge is too high for co-existence with the existing valley slope and valley fill materials. In the process of trying to lower its slope the new Cheslatta River has formed a deeply incised channel on the floor of the glacial trench (Fig. 10a). Its profile is now determined by a series of erosion resistant bedrock sills. The flood plain of the former Cheslatta River has become a terrace, some 5 to 15 m above any potential flood levels. Bed materials range from gravel to boulders; the banks are mostly in glacial till. In terms of Table 1 the imposed changes at the upstream end of the diverison route are Q^+, q_{bm}^-, q_w^-. Along the diverison route this gradually changes to Q^+, q_{bm}^-, q_w^+ and eventually to Q^+, q_{bm}^+, q_w^+, but the latter two changes are transient and will persist only as long as there is considerable erosion taking place along the diversion route. Resulting changes are shown in Table 2. The channel is trying to lower its slope, but reduced sinuosity and accumulation of very coarse lag material on the channel bed have probably resulted in increased slope along much of the diversion route. A large gravel delta has been deposited into Cheslatta Lake. On that delta and immediately above it, the response is a slope reduction, or S^-.

The diversion of the power flows out of the Nechako Reservoir to the Kemano River has had entirely different effects. The power flow of a relatively steady 100–130 m^3 s^{-1} adds 200–290 % to the mean flow of the Kemano River (45 m^3 s^{-1}) at the powerhouse, but represents only 35–45 % of the pre-project 2-yr flood and 19–25 % of the 10-yr flood. The magnitude of the imposed changes decreases significantly along the 16 km diversion route due to local inflow.

The Kemano River is a steep, unstable gravel-bed channel, sinuous, anastamosing, with many mid-channel and diagonal bars. It is confined in a deep, narrow bedrock valley. The valley floor is taken up by fans, debris cones, some flood plain areas and the active channel zone (Fig. 10b). As in the case of the Nechako and Cheslatta rivers, morphologic changes can be documented only on the basis of air photos and some qualitative post-project field observations. In the case of the Kemano River the increased discharge was clearly not large enough to trigger immediate and widespread degradation and incision of the channel. Widening and straightening of the channel were the main changes apparent after 25 yr.

By 1978 channel zone width (including side channels) downstream had increased by 50 %, and was 30 % greater even in the most distal reach. The flood of record is 995 m^3 s^{-1} on October 15, 1974, however, between October 1978 and October 1980 three major floods occurred, the greatest of which was 906 m^3 s^{-1} in November 1978. During this period, degradation of nearly 1 metre occurred at the powerhouse outfall and there is evidence of continuing degradation downstream. The result is that the braided channel is now becoming narrower, more stable, and slightly incised: riparian forest is establishing on the exposed bar tops. By 1982, downstream widths were only 16–26 % greater than before the project.

It is significant that the expected decrease in slope (S^-) or degradation (Table 1, line 1) became obvious only after a quarter century. The cobble-gravel bed of low mobility effectively prevented change until a particularly large flood was able to initiate incision. In the meantime the channel obtained conveyance area by substantial widening of the non-cohesive gravel banks. Table 2 shows the observed direction of change.

After the project was inaugurated, a large increase in production of *Oncorhynchus* salmon was noted in this river. This was possibly associated with the large increase in the extent of flowing side channels due to widening of the channel zone and the much increased, very stable flows. The most recent changes which involve incision of the main channel and abandonment of side channels, might reverse the phenomenon at least partially.

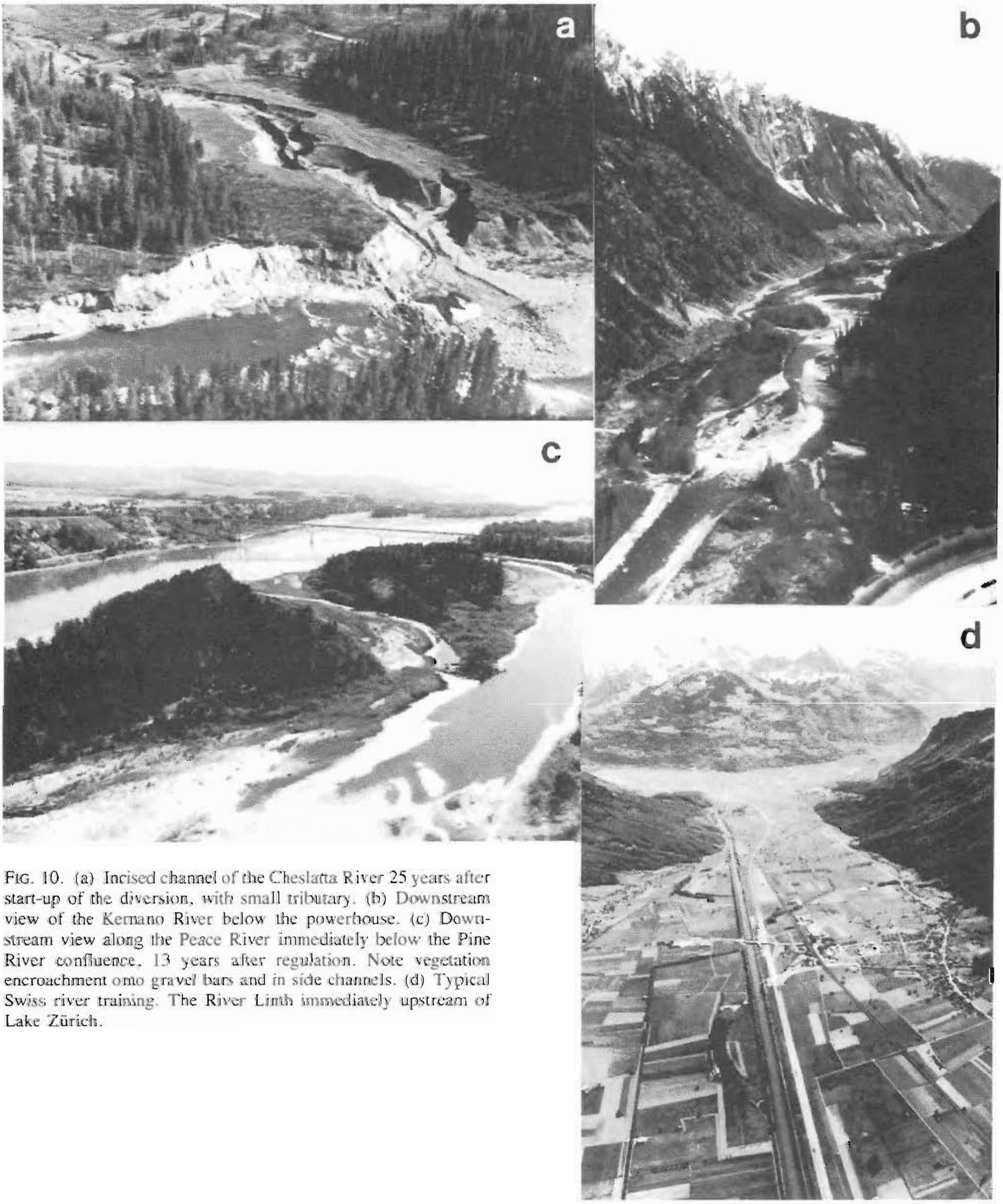


FIG. 10. (a) Incised channel of the Cheslatta River 25 years after start-up of the diversion, with small tributary. (b) Downstream view of the Kemano River below the powerhouse. (c) Downstream view along the Peace River immediately below the Pine River confluence, 13 years after regulation. Note vegetation encroachment onto gravel bars and in side channels. (d) Typical Swiss river training. The River Linth immediately upstream of Lake Zürich.

Flow Regulation

Flow regulation by dam construction usually leads to a reduction in channel forming flows (Q^-) by elimination of flood peaks, even though the total flow volume may remain unchanged. Perhaps more important, sediment transport is completely interrupted at the reservoir (q_{bm}^-, q_s^-). The conventional view of the impact of these changes is that degradation occurs downstream (S^-), as the river recruits a new sediment load. For this to happen, the reduced peak flows in the regulated regime must remain competent to move the bed sediment of the river. In rivers with sand, or perhaps fine gravel beds, this condition in fact occurs. Degradation usually ends relatively soon when a lag deposit of the coarsest material in the bed collects on the surface and armours it. The regulated river cannot move such material. There is considerable experience of cases of this type (Galay 1983 gives a summary of notable cases worldwide) which typically yield one to several metres of bed lowering over many kilometres.

The Peace River, in northern British Columbia (Fig. 10c), has been regulated since 1968 at W.A.C. Bennet Dam near Hudson Hope. Mean annual peak flows in the river have been reduced by about 50% in the 170 km reach downstream to the Alberta border (from 7600 $m^3 s^{-1}$ to 3300 $m^3 s^{-1}$ at the Taylor gauge, 130 km downstream). The Peace River is a cobble-gravel river which exhibits an armoured bed surface at all times — the consequence of sediment transport mechanics for large materials (Parker and Klingeman 1982). Consequently, general degradation should not be expected on this river as the flows are not competent to disturb the material. On the contrary, it may be expected that sediment delivered by the unregulated major tributaries, formerly moved on by the main river during high spring flows, may begin to accumulate in Peace River. Repeated surveys at specific cross-sections confirm these expectations. Aggradation is evident chiefly at the Pine River confluence (mean annual flood, 2000 $m^3 s^{-1}$) at Taylor: this tributary delivers the largest coarse material load of any in the reach.

Equations (1) and (2) predict that the river should eventually become narrower and shallower. For a change of peak flows by a factor of 0.5, width should eventually be reduced by about 30%, and depth by 20–25%. Reduction in width seems to be achieved in three ways:

1) Cobble-gravel bar surfaces, formerly inundated regularly during spring floods, are now abandoned except during exceptional (probably mainly ice jam induced) floods. Primary vegetation succession has begun on these surfaces.

2) Accretion of sand and silt at bar edges along the river builds up additional bar surface. This process is prominent downstream from the Pine River confluence because of the relatively large load of fine material carried in by that tributary. This is, quantitatively, the least important factor of the three. However, it provides a substrate for primary succession along the channel edge dominated by *Salix* spp., quite distinct from that of the river bar tops, where *Populus* sp. establishes in the barren, gravelly soil.

3) Abandonment of secondary channels may be the most important factor. In the natural regime these channels carried significant portions of high flow. Since regulation, their total length along 128 km of the river has been reduced by 56%, from 228 to 160 km.

The last process emphasizes that the channel is undergoing a change from being an irregularly sinuous, frequently split channel toward being a single thread channel which likely will exhibit more regular meandering tendencies. This trend is consistent with the reduction in peak flows and sediment transport, given the channel gradient and material texture. Since 1967 the "braiding index" (total length of channel/main channel length) has decined from 3.26 to 2.25. It will undoubtedly drop farther in succeeding decades but will not reach the limit of 1.0.

The flood plain deposits of the Peace River consist of sands and silts of up 2 or 3 m depth over channel gravels. The sands and silts have accreted by deposition from overbank flooding onto bars where vegetation had become established. The regulated flows will not allow this process to continue. The substantial area definitively exposed by regulation will accrete only a thin veneer of fine sediments over channel gravels. This may substantially alter vegetation succession. Further, this surface will remain at a lower elevation than the former flood plain, which will appear to be a 1 or 2 m high terrace by comparison. Ice jam floods will irregularly inundate both the recently exposed surface and, perhaps, sections of the flood plain. However, the sedimentological effects of this flooding will be far less substantial or consistent than those of the former spring floods. Due to the winter water temperature of +1 to +2 degrees Celsius at the powerhouse, the river is permanently ice free for at least 50 km below the powerhouse.

Habitat impacts include the changed river edge environment associated with the new pattern of sedimentation and vegetation succession, and the loss of extensive areas of shallow secondary channel area.

The North Saskatchewan River below Big Horn Dam in Alberta, Canada is a particularly interesting case of regulation because it involves severe regulation of a very unstable, braided gravel bed channel. The mean annual flood has been reduced from 450 $m^3 s^{-1}$ with a standard deviation of ± 50 $m^3 s^{-1}$ to 168 ± 5 $m^3 s^{-1}$, which more or less corresponds to the full-gate flow of the powerhouse. The project has only an emergency spillway which is unlikely ever to be used. The mean annual flow is unaffected at 73 $m^3 s^{-1}$. The project became operational in 1972.

Unfortunately there has been no systematic study of downstream effects so far and pre-project data are limited to the usual air photo coverage. There has not been any significant degradation. The downstream morphology has changed drastically from highly braided to anastomosed. Because of the dry climate and high elevation of the project area, the former braided channel zone is revegetating only slowly. Many formerly active side channels are now dry but often have been dammed by beavers.

River Encroachments and River Training for Flood Control and Navigation

The discussion of morphologic change has, so far, been confined to the downstream effects of various man-made interferences with river flow or with the sediment load of rivers. Several of the morphologic parameters that are treated as "dependent" in Table 1 are, however, also subject to direct man-made modification, which then leads to indirect effects on other parameters. Channel encroachments and river training works constitute such direct interference with channel morphology. They generally involve direct, imposed modification of w, but λ and P might also be changed directly. The resulting changes in d, S, D_{50}, F, M, and q_{bm} (Q and q_w are not normally affected) are, in general, more predictable than the types of changes addressed by Tables 1 and 2.

Most encroachments are associated with bridges, dikes, or highway and railway embankments paralleling a river. They do not normally result in morphologic changes much beyond the immediate project area but, particularly from a fisheries viewpoint, there can be severe detrimental effects due to changes in habitat along the encroachment riverbank, irregularities and eddies and increased near-bank velocities. Most of these problems can be mitigated at relatively little cost but this often requires departures from standard engineering practice and therein lies the main problem

(Kellerhals et al. 1985). The biologists charged with protecting the resource often lack the knowledge to question established engineering design practice or to suggest less damaging solutions.

Large-scale river training of split, anastomosing and braided gravel-bed rivers is primarily a European phenomenon. Many hundreds of kilometres of such rivers have been forced into straight or gently curving channels between rigid rip-rap, concrete, or stone masonry banks (Fig. 10d). Often the trained channels are exceedingly narrow to induce bed degradation and to overcome any tendancy towards forming alternating gravel bars. Bed elevation and bed form are the only remaining self-adjusting morphological parameters in such channels. The relative bed load, q_{bm}, tends to increase somewhat because large areas of sediment deposition are eliminated by these training schemes.

River training for navigation purposes is affecting many of the world's largest rivers to some degree. The morphological effects can vary greatly but the general trend is usually toward narrower and shorter channels of reasonably trapezoidal cross section. Figure 9 illustrates how such a trend from natural, often triangular sections towards trapezoidal ones can result in a significant loss of areas of shallow depth and low velocity.

Perspective Discussion

In this paper we have introduced the morphology of large rivers by reviewing contemporary descriptive classifications of river channel form. These depart from classical approaches, which summarized channels into only a few comprehensive types (meandered, braided), by separately categorizing each major morphological element. This provides both a more sensitive indication of the response of the river to its governing conditions and a means to provide a practical description of the geophysical aspects of riverine habitat.

The major factors governing river behaviour are the water and sediment supply, and the physiographic setting and materials through which the river flows. Riparian vegetation and local climate are secondary factors important in certain contexts. The most universal perturbing agency in the short term is human activity. In an ideal alluvial river — that is, one flowing entirely in its own deposits — all of the morphological response elements are determined by these factors. In fact, in most rivers, one or another morphological parameter is imposed, frequently it is the slope. Furthermore, hydraulic relations in rivers are so complex that they are not perfectly known: sediment transport in particular remains a vexing issue.

Empirical characterization of river morphology and behaviour, summarized in "hydraulic geometry", can be used to estimate flow parameters in reconnaissance investigations, and can be used to extend physical habitat descriptions. In the second case, far more attention must be paid to secondary channels, side channels, deltaic distributary channels and flood plain lakes that often privde the richest biological habitat.

Because of imperfect knowledge of river behaviour and the complexity of imposed and response conditions, the overall assessment of morphological changes due to human disturbance is, in general, a qualitative exercise. Because of this, case histories are of critical importance for improving experience. Until rather recently, such cases were rarely reported. Major engineering projects, in which river regime or morphology is deliberately disturbed, are carried out in two distinct phases. Design and construction are supervised by engineers with specialist knowledge of river behaviour and the capability to observe and understand the significance of subsequent changes in the river. Once the operation and security of the major installations are assured, however, these people leave the project. Operating personnel, present for years and able to observe the changes, are rarely trained to record them or to understand their significance. The problem is made more difficult on large rivers, where important changes may occur imperceptibly over decades or centuries; that is, beyond any effective planning horizons.

To the extent that this situation is changing, it is in a major degree due to increased concern for the maintenance of aquatic habitat for fish. In Canada, the most effective river management regulations stem from the federal Department of Fisheries and Oceans and certain provincial fisheries management programmes. This has substantially improved the opportunity to forecast river channel changes that will accompany major projects, attempts to mitigate them, and the occasion to observe the actual effects. Another development has occurred, however. The effective scientist-managers in fisheries management programmes usually are biologists. Most are not — except by accumulated experience — well versed in river behaviour. We have observed the re-invention of many wheels as the result of this situation. We close the paper, then, with two simple pleas:

1) that river managers, prominent amongst them fisheries biologists, recognize the importance of documenting and publishing complete case histories of changes in large rivers, and attempt to encourage this activity whenever possible (e.g., by incorporating long-term monitoring in the terms of approval for major projects);

ii) that we all recognize the full complexity of the ecosystem that rivers represent, including its geophysical basis, and cooperate to ensure that the best experience is brought to bear on each aspect of the analysis of river systems.

References

ANDERSON, R.J., AND D.K. MCKAY. 1973. Seasonal distribution of flow in the Mackenzie delta, N.W.T., p. 71–110. *In* Hydrologic aspects of northern pipeline development. Canada, Environmental Social Committee, Northern Pipelines, Task Force on Northern Oil Development. Report 73-3.

BRAY, D.I. 1973. Regime relations for Alberta gravel-bed rivers. Can. Hydrol. Symp. Proc. 7: 440–452.

BLENCH, T. 1969. Mobile-bed fluviology. University of Alberta Press, Edmonton, Alta. 168 p.

BRICE, J.C. 1982. Stream channel stability assessment. U.S. Dept. of Transportation, Federal Highway Administration. 48 p.

CHURCH, M., AND R. GILBERT. 1975. Proglacial fluvial and lacustrine environments, p. 22–100. *In* A.V. Jopling and B.C. McDonald. [ed.] Glaciofluvial and glaciolacustrine sedimentation. Soc. Econ. Paleontol. Mineral. Spec. Publ. 23.

CHURCH, M., AND M.J. MILES. 1982. Processes and mechanisms of bank erosion: discussion, p. 259–268. *In* R.D. Hey, J.C. Bathurst, and C.R. Thorne [ed.] Gravel-bed rivers. Wiley, Chichester, UK.

Davis, W.M. 1899. The geographical cycle. Geograph. J. 14: 481–504.

Dunne, T., and L.B. Leopold. 1978. Water in environmental planning. W.H. Freeman and Company, San Francisco, CA. 818 p.

Fahnestock, R.K. 1963. Morphology and hydrology of a glacial stream — White River, Mount Rainier, Washington. U.S. Geol. Surv. Prof. Pap. 422–A: 70 p.

Galay, V.J. 1967. Observed forms of bed roughness in an unstable gravel river. Proc. 12th Congr. Int. Assoc. Hydr. Res. v.1: 85–94.

1983. Causes of river bed degradation. Water Resour. Res. 19: 1057–1090.

Galay, V.J., D.B. Tutt, and R. Kellerhals. 1983. The meandering distributary channels of the upper Columbia River, p. 113–125. *In* River Meandering: Proceedings of the Conference Rivers '83. American Society of Civil Engineers, Waterway, Port, Coastal and Ocean Division.

Hickin, E.J. 1984. Vegetation and river channel dynamics. Can. Geogr. 28:111–126.

Holz, R.K., V.R. Baker, S.M. Sutton, Jr., and M.M. Penteado-Orellana. 1979. South American river morphology and hydrology, NASA Spec. Publ. 412, v. 2: 545–594.

Jolly, J.P., M.J.R. Pitchen, S.I. Solomon, and A. Waroway. 1977. Flood magnitude determination from channel width measurements, p. 45–49. *In* Can. Soc. for Civil Eng. Third National Hydrotech. Conf. Proceedings, Quebec

Kellerhals, R. 1967. Stable channels with gravel-paved beds. Am. Soc. Civil Eng. J. Waterways Harbours Div. 93 (WWI): 63–84.

Kellerhals, R., M. Church, and D.I. Bray. 1976. Classification and analysis of river processes. Am. Soc. Civil Eng. J. Hydraulics Div. 102: 813–829.

Kellerhals, R., M. Church, and L.B. Davies. 1979. Morphological effects of interbasin river diversions. Can. J. Civil Eng. 6: 18–31.

Kellerhals, R., and M. Church. 1980. Comment on "Effects of channel enlargement by river ice processes on bankfull discharge in Alberta, Canada" by D.G. Smith. Water Resour. Res. 16: 1131–1134.

Kellerhals, R., M.J. Miles, and G.C. Seagel. 1985. River channel encroachments by highways and railways, p.77–96. *In* Can. Soc. for Civil Eng. Annual Conference and 7th Canadian Hydrotechnical Conference, Proceedings Vol. 1B.

Knighton, A.D. 1974. Variations in width-discharge relation and some implications for hydraulic geometry. Geol. Soc. Am. Bull. 85: 1069–1076.

Lacey, G. 1930. Stable channels in alluvium. Inst. of Civil Eng. Proc. 229: 281–290.

Lane, E.W. 1955. The importance of fluvial morphology in hydraulic engineering. Am. Soc. Civil Eng. Proc. 81 (July): 745-1 to 745-17.

Langbein, W.B. 1963. The hydraulic geometry of a shallow estuary. Int. Assoc. Sci. Hydrol. Bull. 8: 84–94.

Leopold L.B., and T. Maddock, Jr. 1953. The hydraulic geometry of stream channels and some physiographic implications. U.S. Geol. Surv. Prof. Pap. 252: 57 p.

Leopold, L.B., and M.G. Wolman. 1957. River channel patterns: braided, meandering and straight. U.S. Geol. Surv. Prof. Pap. 282-B: 39–85.

McLean, D.G., and M. Church. 1986. A re-examination of sediment transport observations in the lower Fraser River. Environment Canada, Inland Waters Directorate, Water Resources Branch, Sediment Survey. Report IWD-HQ-WRB-SS-86-6. 107 p.

Meade, R.F., C.F. Nordin, Jr, D.P. Hernandez, B. Abel Mejia, and J.M. Perez Godoy. 1983. Sediment and water discharge in Rio Orinoco, Venezuela and Colombia, p. 1134–1144. *In* 2nd Int. Symp. on River Sedimentation, Proc. Beijing, Water Resources and Electric Power Press.

Mollard, J.D. 1973. Air photo interpretation of fluvial features. Can. Hydrol. Symp. Proc. 7: 341–380.

Nanson, G.C., and E.J Hickin. 1986. A statistical analysis of bank erosion and channel migration in western Canada. Geol. Soc. Am. Bull. 97: 497–504.

Neill, C.R. 1973. Hydraulic geometry of sand rivers in Alberta. Am. Soc. Civil Eng. J. Waterways Harbours Div. 93: 453–461.

1987. Sediment balance considerations linking long-term transport and channel processes, p. 255–240. *In* C.R. Thorne, J.C. Bathurst, and R.D. Hey [ed.] Sediment transport in gravel-bed rivers. Wiley, Chichester, UK.

Neill, C.R., and V.J. Galay. 1967. Systematic evaluation of river regime. Am. Soc. Civil Eng. J. Waterways Harbours Div. 93: 25–53.

Paris, E. 1984. River bed response to man-made changes. Inst. of Civil Eng. Proc. 77: 67–77.

Parker, G., and P.C. Klingeman. 1982. On why gravel bed streams are paved. Water Resour. Res. 18: 1409–1423.

Potter, P.E. 1978. Significance and origin of big rivers. J. Geol. 86: 13–33.

Savat, J. 1975. Some morphological and hydraulic characteristics of river-patterns in the Zaire basin. Catena 2: 161–180.

Schumm, S.A. 1977. The fluvial system. Wiley, NY. 338 p.

1985. Patterns of alluvial rivers. Annu. Rev. Earth Planetary Sci. 13: 5–27.

Simons, D.B., and M.L. Albertson. 1960. Uniform water conveyance channels in alluvial material. Am. Soc. Civil Eng. J. Hydraulics Div. 86 (HY5): 33–71.

Simons, D.B., E.V. Richardson, and C.F. Nordin. 1965. Sedimentary structures generated by flow in alluvial channels, p. 34–52. *In* G.V. Middleton [ed.] Primary Sedimentary Structures and their Hydrodynamic Interpretation. Soc. Econ. Paleontol. Mineral. Spec. Publ. 12.

Stalnaker, C.B., R.T. Milhous, and K.D.Bovee. 1989. Hydrology and hydraulics applied to fishery management in large rivers, p. 13–30. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Strahler, A.N. 1952. Hypsometric (area-altitude) analysis of erosional topography. Bull. Geol. Soc. Am. 63: 1117–1142.

Thomas, W.A. 1977. Hydrologic engineering methods for water resources development. Vol. 12. Sediment Transport. Hydrol. Eng. Centre, Corps of Engineers, U.S. Army, Davis California.

Vanoni, V.A. [ed.]. 1975. Sedimentation engineering. Am. Soc. Civil Eng., New York. 745 p.

Welcomme, R.L. 1985. River fisheries. FAO Fish. Tech. Pap. 262, Rome. 330 p.

The River Continuum Concept: A Basis for the Expected Ecosystem Behavior of Very Large Rivers?

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Abstract

SEDELL, J. R., J. E. RICHEY, AND F.J. SWANSON. 1989. The river continuum concept: A basis for the expected ecosystem behavior of very large rivers?, p. 49–55. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The river continuum concept (RCC) is examined to determine its usefulness in predicting the behavior of large river ecosystems. Although some verification of RCC predictions of carbon dynamics in large rivers has been noted, most large-floodplain river systems cannot be adequately addressed using the RCC as originally defined. In the world's largest rivers, the importance of upstream carbon to the carbon utilized in downstream reaches is debatable, implying that river zones may take on a life of their own within a basin. Hydrologic interaction of a river with its streamside forest and floodplain is critical for carbon-processing and fish habitat regardless of size of the drainage basin. Our present ability to evaluate big-river biotic assemblages and ecosystem metabolic interactions is significantly limited by an inability to cope meaningfully with the complexities associated with spatial and temporal heterogeneity along the length of the river.

Résumé

SEDELL, J. R., J. E. RICHEY, AND F.J. SWANSON. 1989. The river continuum concept: A basis for the expected ecosystem behavior of very large rivers?, p. 49–55. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Les auteurs évaluent l'utilité du concept de la continuité dans un cours d'eau (RCC) pour prévoir le comportement d'écosystèmes de grandes rivières et de fleuves. Bien que certaines prédictions du RCC concernant la dynamique du carbone dans les grands cours d'eau aient été exactes, le RCC ne peut servir, tel qu'il a été défini au départ, pour la plupart des systèmes fluviaux à larges plaines inondables. Le rapport entre le carbone des cours supérieurs et le carbone utilisé dans les cours inférieurs des plus grands fleuves du monde est discutable; cela voudrait dire que les diverses zones d'un cours d'eau peuvent être indépendantes les unes des autres. Les interactions hydrologiques entre un cours d'eau et la forêt ou la plaine inondable qui le borde sont primordiales, en ce qui concerne la dynamique du carbone et l'habitat des poissons, peu importe la taille du bassin hydrographique. À l'heure actuelle, nos capacités à évaluer les assemblages biotiques fluviaux et les rapports métaboliques dans un écosystème sont grandement limitées par notre incapacité à comprendre les complexités associées à l'hétérogénéité spatiale et temporelle le long du cours d'eau.

Introduction

Large rivers have not been as well studied from an ecosystem perspective as have small streams (Richey 1981; Naiman 1983a; Decamps 1984a). The most dramatic and predictable ecological changes occur between small streams and intermediate-sized fourth to sixth-order rivers. These changes occur within the first 200 km of river length, whereas large rivers flow for thousands of kilometres with little predictable change but with the greatest production and exploitation of fisheries resources (Welcomme 1985). Large rivers are viewed as separate systems with a different set of ecological characteristics and management problems than upstream rivers or their valleys (Lavandier and Decamps 1983); therefore, it may not be plausible to extrapolate concepts of riverine ecosystem function applicable to upper river stretches to downstream areas. Dams, lakes, and swamps serve as "discontinuities" dividing rivers into more or less independent reaches (Ward and Stanford 1983; Decamps 1984b). Variation in the extent of large river floodplains and transverse interactions between river and floodplain forests often dominate longitudinal characteristics of riverine ecosystems (Hynes 1985; Welcomme 1979; Junk et al. 1989; Pautou and Decamps 1985; Bravard et al. 1986; Amoros et al. 1987; Ward and Stanford 1989).

One of the most provocative concepts of longitudinal variation in riverine ecosystem characteristics is the river continuum concept [RCC] (Vannote et al. 1980; Minshall et al. 1985). The RCC treats the river network as a continuously integrated series of physical adjustments and resource gradients along which the biota and ecosystem processes are adjusted, using a hypothetical river system in a temperate forest basin as an example. River networks are viewed as longitudinally linked systems in which biotic assemblages are orderly, and ecosystem-level processes in downstream reaches are linked to those in upstream parts of the network. Subsequently, the concept has produced a great deal of lively discussion — exceptions were pointed out, new studies were initiated to evaluate its usefulness as a generalizable concept, and calls for clarifying the definition and basic tenets of the concept were heard (Statzner and Higler 1985).

For both small and large basins, problems with the RCC quickly arose. River systems are not continuous physical and biological gradients to the sea (Balon and Stewart 1983; Statzner and Higler 1985), dense riparian vegetation does not exist around many headwaters at high altitudes (Ward and Stanford 1983), and biotic assemblages do not match the functionally defined progression in responses to stream order (Winterbourn et al. 1981; Benke et al. 1984; Bruns et al. 1984).

The relevance of the river continuum concept to large rivers is dependent on what characteristics or processes one is interested in — carbon flow, nutrient cycling, biotic assemblage diversity, standing crop, or fish productivity. In this paper, we: (1) examine RCC ecosystem predictions for large rivers; (2) test these with the Moisie River, a large Canadian boreal river, the South American Amazon River, the largest river in the world and the Parana–Plata River system, and (3) consider the appropriate theoretical basis for analysis of large rivers.

Whether we view a river system as composed of a tightly integrated series of biotic and ecosystem changes from headwaters to the sea or a set of geomorphically and biotically independent reaches depends on the river system studied, the investigators' research approach, and system characteristic of interest. A river ecosystem approach must incorporate both concepts to describe adequately and account for physical and biological processes. Linking geomorphically distinct reaches functionally into a longitudinal perspective is the research challenge.

RCC Predictions of Carbon Dynamics for Large Rivers

The original RCC was not specific in its predictions of the behavior of large rivers. Most subsequent discussion focused on smaller river systems, and the complexity of large rivers was overlooked. Nonetheless, Vannote et al. (1980) and Minshall et al. (1985) addressed big rivers to make some relevant predictions of carbon dynamics. The set of carbon dynamics that can be predicted includes:

Prediction 1 — Carbon Sources

Carbon in the main channel of a large river results from various terrestrial and aquatic sources:

a) Large rivers receive the majority of their fine particulate organic carbon (FPOC) load from upstream processing of dead leaves and woody debris because the immediate effects of adjacent riparian vegetation are minimal. Thus, the ratio of coarse to fine particulate organic carbon is expected to be very small (CPOC/FPOC < 0.001).

b) Fine particulate detritus is also entrained from the floodplain during floods and through lateral migration of the channel.

c) Aquatic primary production is limited by depth and turbidity, so respiration exceeds production ($P/R < 1$).

Prediction 2 — Carbon Processing

a) The heterotrophic use and physical absorption of labile dissolved organic carbon (DOC) are rapid in headwater regions; thus, DOC in the larger downstream rivers should have higher molecular weights and be more refractory. A similar pattern of increasing refractivity would be expected for POC.

b) The rate of within-system processing increases and the rate of storage and export decreases with increasing substrate quality and duration in the river.

Prediction 3 — Stability of Energy Flow

The minimization of the variance in energy flow is the outcome of overlapping seasonal variations of detrital and primary production inputs, adjustment of functional groups over time, and the organic and inorganic matter transport and storage characteristics of rivers. As the sum of these factors, within-river oxidation is relatively constant over time and space.

Few studies on large rivers have been conducted with sufficient resolution to test these concepts. We now consider two large-river systems with sufficient data to do so (Table 1).

Moisie River

Naiman (1982, 1983a, 1983b, 1983c) demonstrated that with increasing channel size in a subarctic river of 20000 km^2 (Moisie River, Quebec, Canada, mean annual discharge = 470 m^{3}s^{-1}) carbon processing could be explained by simple power functions relating the parameters of interest (community respiration, periphyton production, seston transport, DOC and POC storage) to stream order. The Moisie drainage basin has numerous lakes, bogs, and beaver dams in its upper watershed. The river system has no floodplains and is a geologically constrained riffle-pool channel. Stream order was a very useful physical parameter in the river basin because it was possible to relate stream order with great accuracy to watershed area, mean annual discharge, and channel width. This study provided unequivocal support to the RCC projections on carbon dynamics and suggested the importance of upstream carbon supply to downstream metabolism.

TABLE 1. Summary of carbon dynamics for two large rivers, subarctic Moisie River, Canada, North America, and tropical Amazon River, Brazil, South America.

	Moisie River (2×10^5 km^2)	Amazon River (6×10^6 km^2)
Carbon Sources	upstream refractory carbon and river inchannel autotrophs	allochthonous vascular plants from lowland areas, no river channel carbon,
Carbon Processing	annually high due to autotrophs, geomorphic areas not examined for carbon processing, spiral length longer than 9th order reach length	refractory carbon processing over 100's km, respiration rapid in distinct geomorphic regions (10's km) from undetermined channel margin sources.
Stability of Carbon Energy	upstream carbon subsidy and large river summer autotrophic production in channel. Temperature controlled in winter	relatively uniform in composition and amount, 2 fold annual variability in respiration.

Moisie River Carbon Sources

Naiman (1983a) and Connors and Naiman (1984) found an unequivocal transition between streams dominated by allochthonous inputs (orders 1–3) and those dominated by autotrophic inputs (> order 4). As channel size increased, there was the predicted decrease in allochthonous inputs and an increase in gross production by mosses, macrophytes, and periphyton. The 9th order river segment received a large input from in-channel moss production.

Moisie River Carbon Processing

Naiman (1983a, 1983b) found that respiration rates increased with stream-size increase. Most of the respiration came from autotrophic respiration. Within-stream processing increased with increasing substrate quality derived from the autotrophs. Storage of organic material decreased with stream-size increase.

Moisie River Stability of Energy Flow

From the published accounts of the carbon dynamics of the Moisie River, it is not yet possible to determine if within-river oxidation is constant over time and space. From the respiration data, it appears as if the upstream reaches subsidize the downstream reaches to a certain extent (Naiman et al. 1987).

Moisie River Summary

This large, subarctic river with negligible floodplain areas but with many bogs and lakes in its basin follows the RCC predictions on carbon processing (Table 1). A problem with extrapolating to other rivers is that the length of the 9th-order river reach is less than 100 km and floodplains does not exist along the river. Nonetheless, the Moisie River represents one of the best studied large-river ecosystems to date. The 9th order Salmon River in Idaho (Minshall et al. 1983) is a geologically constrained, clear water, pool-riffle channel. It also exhibits similar carbon characteristics as the Moisie River.

Amazon and Parana-Plata River Systems

The CAMREX (Carbon in the Amazon River Experiment) project measured the distributions and composition of carbon as a function of geomorphology and hydrology over a 2 000-km stretch of the Amazon River on nine cruises at different stages of the hydrograph. On the basis of reported results (Ertel et al. 1986; Hedges et al. 1986a, 1986b; Richey et al. 1986; Devol et al. 1987) we can examine the RCC (Table 1).

Amazon Carbon Sources

The POC has an almost constant composition over time and space in the Amazon mainstem. The fine particulates (< 0.063 mm) are predominantly degraded, N-rich soil organic matter, whereas the coarse fraction (> 0.063 mm) is recent, diagenetically unaltered vascular plant material (about 80 % leaf and 20 % wood). Stable carbon isotopes indicate that some of this material is probably derived from within the lowland basin and not in the headwaters. The DOC — about 50 % of the total organic carbon — averages 60 % humic materials (balance unknown), with the fulvic and humic acid fractions having distinct compositions and residence times within different parts of the basin. Dissolved humic acids introduced by blackwater tributaries are preferentially adsorbed onto mainstem fine particulates. Macrophyte remains constitute no more than 10 % of the total organic matter. There is no consistent downstream increase in refractory organic components or simplification of organic composition in the particulates.

Amazon Carbon Processing

The riverine carbon pools have a significant component of recent carbon, indicating carbon cycling times within the Amazon basin of < 150 yr for all but the fine particulate fraction (< 600 yr). High rates of respiration occur within the river, supported by organic material of an as yet undetermined lateral source and composition. These exchanges take place most actively in several distinct geomorphological regions where floodplain waters interact with mainstream water, and are characterized by carbon and water mass balance anomalies. Most respiratory CO_2 is lost to the atmosphere, which is a major sink for riverine carbon.

Amazon Stability of Energy Flow

Deciding whether in-river oxidation in the Amazon basin is constant over time and space is subjective. Respiration per unit volume varies over the annual hydrograph by a factor of two. Attainment of equilibrium depends on the various time and space scales of water routing, sediment transport, and chemical cycling. The systematic variability of water and element distributions is observable on the order of weeks. According to the properties of each substance, relevant length scales range from hundreds of kilometres up- and down river (conservative substances) to tens of kilometres (less conservative substances) to lateral exchange with the varzea (more labile substances).

Clearly, the Amazon does not conform precisely to the original tenets of the RCC. However, the principal distributions of carbon are controlled by the geomorphology and hydraulics of the system, which are central points of the RCC. Lateral exchange with the floodplain has a significant effect on the mainstem carbon abundance and oxidation. Big rivers can be divided up into metabolically discrete zones or patches. They do not form a simple, direct spatial continuum of organic processing from headwaters to the sea, because of discontinuities in landforms and hydraulics that constrain river–forest–varzea interactions.

Parana–Plata River System

The Parana–Plata River system, the neighboring drainage basin south of the Amazon, is the only major floodplain river where a longitudinal relationship of fish biomass with river organic material and nutrients has been demonstrated. Quiros and Baigun (1985) regressed fish biomass and catch per unit effort against total organic nitrogen and against total organic carbon and found that much of the spatial variability in fish abundance in the Parana River is explained by the content of organic matter in the water column. Island lagoons under greater influence from the main river channel showed smaller fish biomass than those near the margins of the floodplain, where they are influenced by secondary channels and lateral tributaries with more organic matter. In aquatic environments with low nutrient concentrations, the positive relationship between levels of organic matter in the water column and fish abundance might not be found.

Quiros and Cuch (1989) found a longitudinal increase in nutrients, zooplankton, benthos, fish, and organic matter both in the water column and bottom sediments in the main channel of the upper Parana. Thus the Plata River appeared to be spatially structured along a longitudinal continuum as well as a lateral one across the floodplain.

Amazon/Parana–Plata Summary

These results are not viewed by us as a verification of the RCC. They do point out the common theme of distinct reaches within big-river systems that vary in structural complexity, nutrient richness, and fish biomass. The most productive areas are those most interactive with the floodplains, and geomorphic features determine the extent and duration of this interaction in predictable ways.

RCC, Geomorphology, and River–Forest Interactions

From these and other studies (Minshall et al. 1983, and Naiman et al. 1987) we observe that the RCC provides the most useful predictions of longitudinal lotic ecosystem characteristics for river systems with geological constraints on the extent of forest–river interactions. In unconstrained areas with extensive river–floodplain forest interaction, such as in the Amazon and other large rivers (Welcomme 1979; Bayley and Petrere 1989; Junk et al. 1989; and Quiros and Cuch 1989), productivity of the riparian forest and processes distinctive to the flooded forest environment can greatly modify the longitudinal patterns of ecosystem processes predicted by the RCC.

We agree with Welcomme (1979) and Bravard et al. (1986) that ultimately the significance of floodplain forest effects on river ecosystems can be predicted based on geomorphic and hydrologic constraints on the duration and areal extent of these interactions. A useful approach may be to delineate river reaches on the basis of the lateral extent of floodplain scaled in relation to channel width (floodplain width/bankfull channel width). One might expect a progressive decrease in constraint on floodplain width in a downstream direction. This would follow from the typical decrease in gradient and increase in sediment deposition in downstream areas. However, the distribution of constrained and unconstrained reaches does not vary uniformly along river systems. For example, in the Zaire River system in Africa lower river reaches are highly constrained by bedrock and the river course follows fault lines (Savat 1975; and Balon and Stewart 1983).

In fluvial systems ranging from small streams to large rivers we observe great variation in this floodplain width index resulting from constraints imposed by bedrock outcrops, fans and deltas constructed at the mouths of tributaries, landslides, and other features. In steep, mountain rivers unconstrained reaches may be only 0.5–10 km in length. In contrast, the entire lower 2 000 km of the Amazon River is unconstrained, although there is significant variation in river pattern and interaction with floodplain forest over this part of the river system (Mertes 1986). Unconstrained river reaches typically have multiple secondary channels and extensive area of forest–river interaction caused both by high bank coefficient ratio of streambank:valley floor length and by a broad area of inundation during floods.

The concept of a "bank coefficient" or perimeter index (Gosse 1963) is very useful to river ecologists. This ratio is high where there are many islands and irregular banks. Gosse (1963), with particular reference to the central basin of the Zaire River, suggests that fish production is strongly related to the number and sizes of forested islands present in a given reach. Gosse stresses the importance of island development in improving habitat heterogeneity (depth, substrate, current) and enhancing trophic conditions. For the lower 2 000 km of the Amazon River, Mertes (1986) found that areas containing the largest number of islands corresponded with the areas of highest lateral migration. Sedell and Froggatt (1984), Minshall et al. (1985), and others have noted that in these areas carbon storage and riparian inputs, as well as area inundated, are greater than in single channels, implying greater productivity.

River reaches with a high "bank coefficient" index or perimeter index usually occur in hydraulic transition zones, such as changes in gradient. Neither studies of ecosystem production parameters (respiration, allochthonous inputs, gas dynamics, nutrient production) nor of fish fauna have been matched to such a zone of hydraulic change or intense interaction with the riparian vegetation in large floodplain rivers. River ecologists first need to partition the river into broad geomorphic characteristics of a segment, reach, or zone of a river (Amoros et al. 1987) and then determine the biotic community and carbon processing response for channel and floodplain reaches within these reaches.

The interaction of the stream channel with vegetated stream banks or floodplain is important for fish communities regardless of size of stream or river. This interaction represents a factor in both forested and savannah areas that is generally overlooked in large rivers because of the diminished inputs of leaf litter, shading, and stability of a downed tree or snag.

On large floodplains of rivers the hydrologic connectedness of the floodplain to the main river channel and area inundated may determine its productivity. The rate at which water moves onto or off of the floodplain helps determine the type and extent of the nutrient cycling regime (anaeorobic to aerobic). Junk et al. (1989) described river pulsing or the seasonal flood wave as the driving force for the river–floodplain complex, maintaining the complex in a dynamic equilibrium. The flood pulse, preventing permanent stagnation, allows for rapid recycling of organic matter and nutrients, and results in a productivity which is hypothesized to be greater than if the interflood zone were either permanently inundated or dry.

The geomorphic structure and biology of river systems viewed in this way exhibit interesting similarities and differences between headwater streams and large rivers. Both constrained and unconstrained reaches can occur at any drainage area within a basin, but agents leading to their formation may vary. In small and intermediate sized channels, for example, large woody debris can locally raise base level, forming a broad unconstrained reach upstream. Landslides are common agents of constraint in fourth- and fifth -order channels in unstable mountain areas. Constraints along major river valleys are principally bedrock outcrops. Very broad, unconstrained areas with extensive channel development can form at intrariver system deltas.

The hydrology and hence biology of unconstrained reaches varies significantly between headwater streams and river mainstems. Small drainage areas and steep hillslope and channel gradients typical of headwater streams limit the duration of overbank flooding. Under these conditions particulate organic matter can be exchanged between the channel and floodplain forest, but the dominant effects of streamside forests are shading and input of litter and large woody debris directly to the stream channel.

In headwater areas flooding generally does not last long enough for certain floodplain processes to occur. Where floodplain forests, lakes, and secondary channels are flooded for weeks and even months, high levels of aquatic primary and secondary production can occur (Welcomme 1979; Junk et al. 1989). This is possible along large rivers in which exceptionally large drainage areas and low transit time of water can sustain flooding of long duration. Consequently, much of the forest-river interaction in these settings occurs in the flooded forest environment.

Synthesis

Longitudinal variation in river ecosystems can be viewed from several perspectives: (1) the RCC view emphasizes change in carbon processes and invertebrate communities in relation to controls on food resources, (2) a more traditional drainage basin ecosystem approach focuses on the flows of carbon and biogeochemical cycling, (3) fisheries perspectives concern species distributions and productivity in various habitats. The very significant reach-scale variation of river–forest interactions, discussed in this paper, is an integral part of carbon and biogeochemical cycling systems and of the fisheries ecology of rivers of all sizes. However, this type and scale of river ecosystem behavior is not addressed by the RCC. As such, the RCC is of limited value for predicting large river ecosystem function.

Geomorphic conditions in unconstrained river reaches promote interaction of rivers with floodplain forests with potentially dramatic impacts on aquatic processes. The original statement of the RCC recognized along-stream variation in the effect of streamside forest on the channel environment, but did not consider the effect of the flooded forest environment. The ideas of Welcomme (1979), Decamps (1984b), Bravard et al. (1986), and Junk et al. (1988), thus provide concepts that lead to a more robust conceptual view of a river–floodplain system.

Future analysis of river ecosystem structure and function must integrate the RCC to floodplain–forest interactions of the whole hydrosphere (groundwater included). The river floodplain system has already been addressed. What has not been addressed is the linking of individual reaches along the river. What are the ecosystem consequences of different longitudinal arrangements of various hydrologic and geomorphic reaches? Ecosystem dynamics of carbon and nutrients will be affected if adjacent reaches are radically different, e.g., the river flowing from a floodplain reach into a geologically constrained reach. A framework which allows us to examine both the hydrologic and geomorphic settings of the individual reaches and their longitudinal arrangement will make it possible to distinguish the relative merit of viewing a particular river ecosystem as a continuum or as a series of independent reaches. The appropriateness of either of these alternative views is likely to vary with river system structure and with the ecological attribute of interest. For some very conservative attributes of the river ecosystems, reach-scale variation in system structure is of little consequence. Some system attributes, such as fisheries productivity, may vary greatly from reach to reach and within a reach.

Approaches to hierarchical classification (Lotspeich 1980; Frissell et al. 1986; Amoros 1987) help in delineating elements of the system and their relative scales, but stop short of elucidating ecosystem dynamics. The large river system is a sequence of patches of varying lengths and widths, and not a simple continuum. The large river is an accumulation of materials and gases experiencing differing transient times on and off the floodplains to the atmosphere or the sea. The next important step in understanding river ecosystems is to quantify and determine the controls on reach-to-reach interactions of materials, energy, and organisms.

The drainage basin ecosystem approach is accepted for a variety of river studies (Odum 1957; Fisher and Likens 1973; and Hynes 1975). Even in large basins unidirectional flow makes the river dependent upon its headwater streams and integrated subbasins. The distinctive reaches of a big river are also dependent on upstream water, sediment, and some nutrients. An ecosystem approach to large rivers cannot be avoided.

The ecosystem approach to rivers is not as concerned about biotic communities and physical habitat as about energy or carbon flow, nutrient dynamics, and biogeochemical processes linking terrestrial–lotic systems. This is an important point of divergence with the more community and population biologist's approaches to stream and river systems. The ecosystem approach favors mass balance of carbon or nutrients to help identify areas needing study and identifies a set of ecosystem metabolic or nutrient cycling processes used to compare river systems in different geographical regions. Chemistry is the key interface discipline providing a common language for communication and for coordination of concepts and experiments. This approach has been used at the macroscale of the earth to examine linkages between continents, oceans, atmosphere, lakes, and rivers (e.g., global carbon cycling as it is affected by deforestation, agriculture, industrialization, acid rain, and effects of climatic shifts).

The challenge for future research will be to determine how ecologically important processes at the reach levels can be meaningfully aggregated to large river system wide and global-scale responses. How the different spatial and temporal scales can be integrated between and among disciplines (ecosystem scientists, fisheries scientists, biogeochemists, atmospheric scientists, engineers, geomorphologists, and others) is the present challenge.

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References

AMOROS, C., A. L. ROUX, J. L. REYGROBELLET, J. P. BRAVARD, AND G. PAUTOU. 1987. A method for applied ecological studies of fluvial hydrosystems. Regulated Rivers 1: 17–38.

BALON, E. K., AND D. J. STEWART. 1983. Fish assemblages in a river with unusual gradient (Luongo, Africa–Zaire system), reflections on river zonation, and description of another species. Environ. Biol. Fish. 9(3/4): 225–252.

BAYLEY, P. B., AND M. PETRERE, JR. 1989. Amazon fisheries and the aquatic system: current status, p. 385–398. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

BENKE, A. C., T. C. VAN ARSSDALL, JR., D. M. GILLESPIE, AND F. K. PARRISH. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. Ecol. Monogr. 54(1): 25–63

BRAVARD, J. P., C. AMOROS, AND G. PAUTOU. 1986. Impact of civil engineering works on the succession of communities in a fluvial system: a methodological and predictive approach to a section of the Upper Rhone River, France. Oikos 47: 92–111.

BRUNS, D. A., G. W. MINSHALL, C. E. CUSHING, K. W. CUMMINS, J. T. BROCK, AND R. L. VANNOTE. 1984. Tributaries as modifiers of the River Continuum Concept: analysis by polar ordination and regression models. Arch. Hydrobiol. 9: 208–220.

CONNORS, M. E., AND R. J. NAIMAN. 1984. Particulate allochthonous inputs: relationships with stream size in an undisturbed watershed. Can. J. Fish. Aquat. Sci. 41: 1473–1484.

DECAMPS, H. 1984a. Biology of regulated rivers in France, p. 495–514. *In* A. Lillehammer and S. J. Saltveit [ed.] Regulated Rivers. Oslo Univ. Press, Oslo, Norway.

1984b. Towards a landscape ecology of river valleys, *In* T. H. Cooley and F. B. Golley [ed.] Trends in ecological research for the 1980s. Plenum Press, New York, NY.

DEVOL A. H., J. E. RICHEY, P. QUAY, AND L. MARTINELLI. 1987. Dissolved gases and air–water exchange in the Amazon River. Limnol. Oceanogr. 32: 235–248.

ERTEL, J. R., J. I. HEDGES, A. H. DEVOL, J. E. RICHEY, AND M. DEN G. RIBEIRO. 1986. Dissolved humic substances of the Amazon River system. Limnol. Oceanogr. 31(4): 739–754.

FISHER, S. G., AND G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43: 421–439.

FRISSELL, C. A., W. J. LISS, C. E. WARREN, AND M. D. HURLEY. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed contect. Environ. Manage. 10(2): 199–214.

GOSSE, J. P. 1963. Le milieu aquatique et l'ecologie des poissons dans la region de Yangambi. Ann. Mus. R. Afr. Cent. Zool. 116: 113–270.

HEDGES, J. I., W. CLARK, P. O. QUAY, J. E. RICHEY, A. H. DEVOL, AND N. RIBEIRO. 1986a. Composition and fluxes of organic matter in the Amazon River. Limnol. Oceanogr. 31: 739–754.

HEDGES, J. I., J. R. ERTEL, P. O. QUAY, P. M. GROOTES, J. E. RICHEY, A. H. DEVOL, G. W. FARWELL, F. H. SCHMIDT, AND E. SALATI. 1986b. Organic carbon-14 composition in the Amazon River system. Science 231: 1129–1131.

HYNES, H. B. N. 1975. The stream and its valley. Verh. Int. Ver. Limnol. 19: 1–15.

JUNK, W. J., P. B. BAYLEY, AND R. E. SPARKS. 1989. The flood pulse concept in river–floodplain systems, p. 110–127. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

LAVANDIER, P., AND H. DECAMPS. 1983. Ecology of Estaragne, a high mountain stream in the Pyrenees, p. 237–264. *In* B. A. Whitton [ed.] The ecology of European rivers. Blackwell Scientific Publications, Oxford, England.

LOTSPEICH, F. B. 1980. Watersheds as the basic ecosystem: this conceptual framework provides a basis for a natural classification system. N. Am. J. Fish. Manage. 2: 138–149.

MERTES, L. A. 1986. The geomophology and sediment routing of the Amazon River. M. S. thesis, Univ. Washington, Seattle, WA, p. 108.

MINSHALL, G. W., R. C. PETERSEN, K. W. CUMMINS, T. L. BOTT, J. R. SEDELL, C. E. CUSHING, AND R. L. VANNOTE. 1983. Interbiome comparison of stream ecosystem dynamics. Ecol. Monogr. 53(1): 1–25

MINSHALL, G. W., K. W. CUMMINS, R. C. PETERSEN, C. E. CUSHING, D. A. BURNS, J. R. SEDELL, AND R. L. VANNOTE. 1985. Developments in stream ecosystem theory. Can. J. Fish. Aquat. Sci. 42: 1045–1055.

NAIMAN, R. J. 1982. Characteristics of sediment and organic carbon export from pristine boreal forest watersheds. Can. J. Fish. Aquat. Sci. 39: 1699–1718.

1983a. The annual pattern and spatial distribution of aquatic oxygen metabolism in boreal forest watersheds. Ecol. Monogr. 53: 73–94.

1983b. The influence of stream size on the food quality of seston. Can. J. Zool. 61: 1995–2010.

1983c. A geomorphic approach for examining the role of periphyton in large watersheds, p. 191–198. *In* R. G. Wetzel [ed.] Periphyton of freshwater ecosystems. Dr. w. Junk Publishers, The Hague, The Netherlands.

NAIMAN, R. J., J. M. MELILLO, M. A. LOCK, T. E. FORD, AND

S. R. Reice. 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. Ecology 68: 1139–1156.

Odum, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. Ecol. Monogr. 27: 55–112.

Pautou, G., and H. Decamps. 1985. Ecological interactions between the alluvial forests and hydrology of the Upper Rhone. Arch. Hydrobiol. 104: 13–37.

Quiros, R., and C. Baigun. 1985. Fish abundance related to organic matter in the Plata River basin, South America. Trans. Am. Fish. Soc. 114: 377–387.

Quiros, R., and S. Cuch. 1989. The fishery of the lower Plata River basin: fish harvest and limnology, p. 0000–0000. *In* D. P. Dodge [ed.] Proceeding of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Richey, J. E. 1981. Fluxes of organic matter in rivers relative to the global carbon cycle, p. 270–293. *In* Flux of organic carbon by riers to the oceans. U.S. Department of Energy, Springfield, VA. National Technical Information Service CONF-8009140 US 11.

Richey, J. E., R. H. Meade, E. Salati, A. H. Devol, C. F. Nordin, and U. dos Santos. 1986. Water discharge and suspended sediment concentrations in the Amazon River: 1982–1984. Water Res. Res. 22: 756–764.

Savat, J. 1975. Some morphological and hydraulic characteristics of river-patterns in the Zaire basin. Catena 2: 161–180.

Sedell, J. R., and J. L. Froggatt. 1984. The importance of stream-side forests to large rivers: the isolation of the Willamette River, Oregon, U.S.A. from its floodplain by snagging and stream-side forest removal. Verh. Int. Ver. Limnol. 22: 1828–1834.

Statzner, B., and B. Higler. 1985. Questions and comments on the River Continuum Concept. Can. J. Fish. Aquat. Sci. 42: 1038–1044.

1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwater Biol. 16: 127–139.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

Ward, J. V., and J. A. Stanford. 1983. The serial discontinuity concept of lotic ecosystems, p. 29–42. *In* T. D. Fontaine and S. M. Bartell [ed.] Dynamics of lotic ecosystems. Ann Arbor Science Publishers Inc., Ann Arbor, MI.

1989. Riverine ecosystems: the influence of man on catchment dynamics and fish ecology, p. 56–64. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Welcomme, R. L. 1979. Fisheries ecology of floodplain rivers. Longman, London.

1985. River fisheries. FAO Fish. 1985 Tech. Pap., 262: 1–330.

Winterbourn, M. J., J. S. Rounick, and B. Cowie. 1981. Are New Zealand stream ecosystems really different? N. Z. J. Mar. Freshwater Res. 15: 321–328.

Riverine Ecosystems: The Influence of Man on Catchment Dynamics and Fish Ecology

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Abstract

WARD, J. V., AND J. A. STANFORD. 1989. Riverine ecosystems: the influence of man on catchment dynamics and fish ecology, p. 56–64. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Rivers are open systems with interactive pathways along four dimensions: longitudinal (headwater–riverine–estuarine), lateral (riverine–riparian/floodplain), vertical (riverine–groundwater), and temporal (time scales). Man's influence on river ecosystems and riverine fishes may be perceived as disruptions of one or more of these dimensions. Agricultural and forestry practices, by increasing light and nutrient levels, tend to extend the riverine fauna upstream. Dams block migratory pathways, and by altering downstream conditions, induce longitudinal shifts in faunal assemblages. Rivers are straightened, dredged, and confined by levees for purposes of navigation and development of agricultural land. Coupled with reduced flood peaks and lowered groundwater levels from flow regulation and diversion, the river becomes isolated from its floodplain with devastating effects on flood-dependent species of fishes. Patterns of temporal heterogeneity, important to the ecology of riverine fishes, are also subject to anthropogenic alteration. We contend that employing an holistic conceptual framework, including consideration of dynamic interactions along four dimensions, will improve our understanding of the critical components necessary to maintain a productive riverine ecosystem and how these components can be managed to optimize the fishery within constraints posed by multiple-use objectives for the catchment.

Résumé

WARD, J. V., AND J. A. STANFORD. 1989. Riverine ecosystems: the influence of man on catchment dynamics and fish ecology, p. 56–64. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Les rivières sont des systèmes ouverts à parcours interactifs suivant quatre dimensions: longitudinale (origine–rivière–estuaire), latérale (rivière–rive/lit d'inondation), verticale (rivière–eau souterraine) et temporelle (échelles chronologiques). L'influence humaine sur les écosystèmes et les poissons présents en milieu fluvial peut être considérée comme des perturbations d'une ou de plusieurs de ces dimensions. Les méthodes d'exploitation agricole et forestière, qui mènent à une augmentation de l'intensité de la lumière et des teneurs en bioéléments, ont tendance à encourager la dispersion de la faune fluviale vers l'amont. Les barrages bloquent les routes migratoires et mènent à des déplacements longitudinaux des assemblages fauniques en modifiant les conditions de l'habitat d'aval. Le cours des rivières est redressé et dragué tandis que les eaux sont retenues par des digues pour la navigation et l'acquisition de terres agricoles. Des crues moins importantes et de faibles niveaux d'eau souterraine, résultats de la régularisation du débit et de la déviation du cours d'eau, signifient que la rivière devient isolée de son lit d'inondation. Ceci a des incidences dévastatrices sur les espèces de poissons qui dépendent des crues. Les régimes d'hétérogénéité temporelle, importants à l'écologie des poissons fluviaux, sont aussi soumis à une modification anthropogène. Les auteurs soutiennent que l'organisation conceptuelle le holistique, comprenant les interactions dynamiques entre les quatre dimensions, améliorera notre compréhension des composantes critiques nécessaire à la permanence d'un écosystème fluvial productif et révélera comment ces composantes peuvent être gérées afin d'optimiser la pêche en fonction des contraintes imposées par les objectifs d'utilisation multiple du bassin hydrographique.

Rivers are open systems. Unlike lakes that have relatively well-defined boundaries within which the cycling of matter predominates, rivers exhibit strong directionality and are highly interactive with the surrounding landscape of which they are an integral part (Hynes 1975). To perceive rivers as ecosystems necessitates an holistic spatio-temporal framework that includes upstream–downstream linkages, that encompasses the entire river valley, that considers interactions with the groundwater system, and that recognizes the importance of time scales.

River ecosystems and riverine fishes evolved in response to dynamic patterns and processes occurring along four

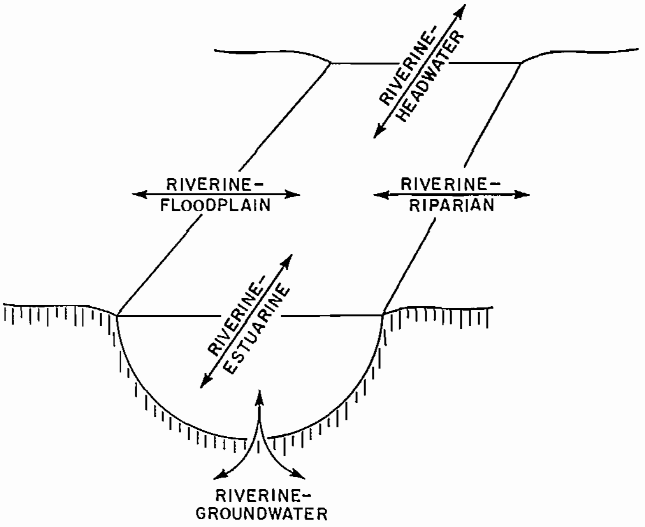

FIG. 1. Major interactive spatial pathways of riverine ecosystems.

dimensions: a longitudinal dimension from headwaters to the sea, a lateral dimension extending beyond the channel boundaries, and a vertical dimension encompassing the groundwater system (Fig. 1), each of which has a temporal dimension. Many of man's activities interfere with the natural dynamics along one or more of these dimensions. The purpose of this paper is to use this four-dimensional perspective to examine the implications of some anthropogenic alterations on catchment dynamics and riverine fishes. It is our contention that such an approach will facilitate attempts to understand the structural and functional attributes of modified riverine ecosystems.

Longitudinal Gradients

The earliest river classification schemes were based on the longitudinal zonation of regional fish faunas (see Hynes 1970a). Illies and Botosaneanu (1963) proposed a universal zonation scheme for river systems. Proponents of the River Continuum Concept (RCC) view downstream changes not as zones, but as resource gradients along which the biota are predictably structured (Vannote et al. 1980). The RCC emphasizes that downstream communities are a function of upstream processes. Whether downstream changes are perceived as clinal or zonal, the fact remains that there are important upstream–downstream linkages in river systems (Ward 1986). For example, the quantity and quality of detritus in a given reach is influenced by the allochthonous inputs, autochthonous production, microbial and animal processing, and retention characteristics of upstream areas. Upstream transfers also occur; migrating fishes, for example, may significantly contribute to the productivity of headwater streams (Hall 1972). Man's activities disrupt the natural patterns of temperature, discharge, water chemistry, organic resources, and habitat heterogeneity along longitudinal profiles.

"Enrichment" from Agriculture and Forest Clearing

Agricultural and forestry practices effectively enrich waters, resulting in upstream extensions of lower riverine conditions (Hynes 1970b). Nutrient loading, greater insolation, and higher maximum temperatures render the affected stream reach more productive than under pristine conditions. Submerged angiosperms may invade the upper reaches (Friedrich and Müller 1984). The enriched stream periodically exhibits oxygen deficits, yet another characteristic of lower reaches that has been extended upstream.

These collective changes eliminate or reduce fish species unable to tolerate the higher temperatures and periodically low oxygen levels. Burton and Odum (1945) documented the upstream displacement of trout following forest clearance that resulted in higher summer water temperatures. Cold stenotherms with high oxygen requirements are displaced toward the headwaters, replacement occurring by the upstream range extensions of fishes formerly restricted to the lower reaches.

Serial Discontinuity

The Serial Discontinuity Concept (SDC) was developed in recognition of the major interruption of longitudinal gradients caused by river regulation and the corresponding upstream or downstream displacement of biotic and abiotic-variables that may occur (Ward and Stanford 1983). The SDC stresses the significance of dam placement along the longitudinal profile (Table 1). The clarifying effect of impoundment, for example, will have little influence on the transparency of an already clear water segment in the upper catchment, whereas a dramatic alteration will occur when the lower reaches of a turbid river are dammed. That the effect of impoundment on a given habitat variable depends on the preimpoundment condition of that variable, which in turn changes along the longitudinal profile, appears obvious but has rarely been recognized.

Because the fish fauna changes markedly along undisturbed river courses, dam position is of great importance in assessing the potential effects of regulation on fishes. Resident fishes in the lower reaches of slowly flowing rivers may find suitable conditions in some reservoirs, but will be less well adapted to the altered habitat conditions in the lotic waters below dams. In contrast, resident fishes of rhithron reaches may better tolerate the altered environment below the dam, but are unlikely to find reservoir conditions suitable. Of course, the special morphology and fauna of

TABLE 1. Hypothetical examples of longitudinal shifts in habitat conditions induced by deep-release storage reservoirs placed in crenon, rhithron, or potamon zones of temperate river systems. Variables below dams may remain generally similar to preimpoundment conditions at that location (—), or may closely resemble conditions that occurred further upstream (←) or downstream (→). Short arrows indicate a shift to conditions of an adjacent zone; long arrows indicate possible crenon-potamon shifts.

	Dam Placement		
Habitat Variable	Crenon	Rhithron	Potamon
Water clarity	—	—	←
Substrate stability	—	—	←
Plankton[a]	⟶	→	—
Maximum temperature	—	←	⟵
Nutrient levels	→	←	←
Nutrient availability	—	—	←

[a] Below surface-release reservoirs.

individual rivers may considerably deviate from general models. The lower Zaire (Congo) River contains a 350 km stretch of turbid rapids inhabited by a diverse fish fauna highly adapted to the torrential conditions (Beadle 1981). Morphological specializations include suctorial mouths, dorsoventrally flattened bodies, enlarged and horizontally positioned pectoral and pelvic fins, and reduced vision. The accessory air-breathing organs characteristic of the Clariidae have been lost by the torrential species of this family, which reside in a permanently well-oxygenated environment. Damming this section of the lower Zaire would most certainly eliminate these highly adapted indigenous fishes as the torrential environment became transformed into an artificial lake, and it is unlikely that most species would find suitable conditions in the regulated river downstream.

The Colorado River below Glen Canyon Dam in the Arizona desert provides an excellent example of a major longitudinal shift caused by regulation. Formerly this was a warm, turbid river containing a fish fauna consisting largely of endemic riverine cyprinids and catostomids (Stanford and Ward 1986a). River regulation has reduced flood extremes, stabilized the bottom, clarified the water, and reduced the annual temperature range from 0–29.5°C to 6–15°C. The rainbow trout (*Salmo gairdneri*) has replaced the squawfish (*Ptychoceilus lucius*), a giant cyprinid, as the top carnivore. The major energy pathway is a simple food web consisting of *Cladophora glomerata*, a filamentous alga that forms dense growths on the stabilized river bottom; *Gammarus lacustris*, an introduced amphipod; and rainbow trout, an exotic salmonid that provides a world-class coldwater recreational fishery in a desert region. In Australia trout have displaced the Murray cod (*Maccullochella peeli*) in summer-cool tailwater environments (Walker 1979).

Impoundments may result in a considerable upstream displacement of plankton. In the River Nile, reservoirs provide a seasonally persistent source of plankton and improve conditions (water clarity, flow stability) for development of plankton below the dams (Talling and Rzóska 1967). Each year up to 30 000 t of planktonic crustaceans pass through the penstocks of a reservoir on the Missouri River (Benson and Cowell 1967), a food resource that is available to riverine fishes directly and indirectly through enhanced invertebrate production.

Migratory Patterns

Longitudinal migrations play a major role in the ecology of riverine fishes and involve movements for breeding, feeding, and overwintering (Nikolsky 1963). Potamodromous and diadromous migrants may move hundreds of kilometres to spawn in small tributary streams, exemplifying the critical importance of the upper reaches for riverine fishes, and the linkage between rivers and estuarine and marine environments.

These longitudinal migrations serve to disperse fish stocks, provide riverine fishes with suitable spawning conditions in habitats where eggs and larvae are exposed to lower predation pressures, enable a more complete use of food resources, allow riverine fishes to use even those headwater areas which disappear during the dry season or which are not productive enough to sustain all life stages. and partition the habitat between species and life stages (Welcomme 1976, 1979; Banks 1969; Hall 1972; Goulding 1980).

Welcomme (1976) estimates that non-riverine lotic segments (stream orders 1–6) contribute over 40 % of the fish catch from African running waters, a production based largely on the upstream migration of riverine species. He states that "the basis of fish catch in such small water courses may also be said to rest on conditions lower down the river" (Welcomme 1976, p. 362); certainly the reverse, a dependence of riverine fish production on conditions in the upper reaches, is also true.

Because migration is a primary functional attribute of rivers, interruptions along the longitudinal dimension will adversely affect the fishery and alter the ecology of the lotic ecosystem. Dams provide the most obvious barriers and may obstruct migration both directly and by altering environmental conditions above and below the dam.

Although the elvers of several species of eels (*Anguilla*) and the gudgeon (*Gobiomorphus coxii*) are capable of surmounting the faces of high dams (Balon 1974; Walker 1985), dams without special passage facilities completely obstruct the upstream migration of the vast majority of fishes. Dams have nearly eliminated many of the "piracema" species from certain Brazilian rivers (Welcomme 1979) and the anadromous species from the Dordogne (Décamps et al. 1979). Once a migratory run has been eliminated, it is difficult to reestablish the fishery from other stocks, apparently because local races are adapted to the specific suite of environmental conditions unique to each river (Banks 1969; Power 1981).

Even where fish passage facilities have been installed, the regulated river may not provide appropriate flows or temperatures to stimulate migration, or ecological barriers (low oxygen levels, gas supersaturation, unsuitable hydraulic design of fish ladders) may prevent or slow movements (Mundie 1979; Banks 1969). Because energy reserves are related to the distances normally traveled by different species or populations of migratory fishes (Nikolsky 1963), delays in reaching spawning grounds can severely reduce spawning success (Banks 1969). Fishes may rely on floods, which are typically suppressed by river regulation (Ward 1982), to reestablish or extend longitudinal distribution patterns (Beumer 1980).

Riverine–Estuarine Linkages

Reduced discharge reslting from diversions and evaporation from reservoirs may disrupt longitudinal interactions between riverine reaches and estuarine and marine waters. Dewatering is especially marked for desert rivers such as the Colorado and the Nile, which have become mere trickles in their lower reaches and are no longer permanently connected to the sea (Rzóska 1976; Stanford and Ward 1986b). Following completion of the Aswan High Dam, fewer nutrients were transported to coastal waters of the Mediterranean Sea, phytoplankton blooms ceased, and *Sardinella* catches declined from 15 000 t in 1964 to 4 600 t in 1965 and to 554 t in 1966 (Aleem 1972).

Modified river discharge results in longitudinal displacement of the freshwater, marine, and brackish faunas. A hydroelectric power station in the lower reaches of the Dnieper reduced or eliminated rheophilic and anadromous fishes, extended the range and increased the abundance of brackish species, and allowed incursions of marine fishes into estuarine reaches (Zalumi 1970).

The Lateral Dimension

The river ecosystem has a lateral dimension that includes the form and dynamics of the channel itself, and interactions between the river and the catchment, especially riparian and floodplain systems (Ward 1988).

Channel Morphology

In much of the world, low gradient rivers have for centuries been managed for navigation, flood control, and land reclamation. Rivers that once flowed in highly dynamic anastomosed drainage networks have been straightened, dredged, and confined to a single channel with little regard for the ecological implications of disrupting natural channel patterns (Décamps et al. 1979; Friedrich and Müller 1984). Managed rivers bear little resemblance to aboriginal rivers, which had many features (shading, depth, water clarity, allochthonous input, habitat heterogeneity, and debris dams) that we have come to associate with reaches further upstream (Cummins et al. 1984).

A complex channel pattern confers numerous benefits on riverine fishes. Backwaters and tributaries provide important refuge, nurseries, spawning and feeding areas (Welcomme 1979; Friedrich and Müller 1984; Bouvet et al. 1985; Stanford and Ward 1986a). Radio-tagging studies demonstrate the ability of endemic riverine fishes of the Colorado River system to locate backwaters under highly turbid conditions and to occupy both natural and man-made side arms during spring runoff (Valdez and Wick 1983). Restoration of fishes in the Rhone River, following periodic reservoir cleaning operations resulting in the downstream passage of muddy anoxic water, is dependent upon recolonization by individuals that escaped the lethal conditions of the main channel by moving into side arms or tributaries (Roux 1984). Side arms provide thermal refuge at times when the temperature of the main channel is unsuitable for certain species (Mosley 1983; Bouvet et al. 1985; Ward 1985).

Gosse (1963), with particular reference to the middle Zaire (Congo) River, suggests that fish production is strongly related to the number and sizes of islands present in a given reach. Gosse stresses the importance of island development in improving habitat heterogeneity (depth, substrate, current) and enhancing trophic conditions; he proposed an index, ''bank coefficient'', to account for the importance of islands in increasing the available shoreline in a river reach.

Pristine rivers contained often massive amounts of wood debris that played a role in structuring channel patterns, and increased habitat complexity and the retention properties of riverine ecosystems (Sedell and Froggatt 1984). Submerged wood substrate comprised only 4 % of total habitat in a Georgia river, yet supported 60 % of the invertebrate biomass and supplied 78 % of drifting invertebrates (Benke et al. 1985). Wood-dwelling invertebrates were heavily utilized as food by most of the large non-piscivorous members of the fish community. Benke et al. (1985) suggest that removal of submerged wood from the river they studied would likely devastate much of the fish community and shift the primary trophic pathway to catostomids and the small fishes that feed on the mud and sand fauna.

The standing crop of fishes may be reduced as much as 98 % by channelization (Karr and Schlosser 1978). In a comparison of fishes in channelized and unchannelized segments of an Australian river, Hortle and Lake (1983) found significantly higher species richness and standing crops at unmodified sites. Species richness and ichthyomass were directly correlated with both the area of submerged wood and the area of slack water.

Rivers are straighted and dredged, and woody debris is removed to accomodate shipping lanes (Rasmussen 1983). In addition, the installation of dikes and levees constricts the main river and isolates side channels and tributaries. Boat traffic itself also impacts the riverine environment and the fishery. Waves generated by passing ships erode river beds and shorelines, increase turbidity, strand small fishes, reduce benthic productivity, reduce macrophytes, and dislodge eggs and larvae. The introduction of steamships to the River'Rhine ''caused heavy damage to the fish fauna by disturbing the fish and especially by destroying the fry. The propellers of ships caused a considerable proportion of the young fish living in the flat groyne fields to be thrown on land'' (Friedrich and Müller 1984, p. 293).

Riverine–Riparian Interactions

The corridors of riparian vegetation along water courses ''are inseparable from the biology in the channel and constitute a ribbon of continuity responsible for many universally discernable (sic) patterns'' (Cummins et al. 1984, p. 1819). Riparian vegetation influences light and temperature regimes; exerts physical control over bank erosion, sediment routing, and channel morphology; contributes organic matter (allochthonous detritus, terrestrial arthropods); and provides cover for fishes directly (overhanging vegetation) and indirectly (bank stabilization, snag habitat).

The potential importance of riverine-riparian interactions has been underestimated, at least for temperate rivers which contain only remnants of their dynamic and anastomosed aboriginal form (Cummins et al. 1984). Natural flooding, that maintained riparian systems in a productive early successional stage, has been suppressed by river regulation, enabling non-riparian species to invade the riparian zone (Décamps 1984; Stanford and Ward 1986b). Logging and overgrazing also markedly alter riparian systems with often devastating effects on the fisheries. Studies conducted on small streams have demonstrated the efficacy of buffer strips (stream side corridors of natural vegetation from which grazing and logging are excluded) in maintaining the integrity of land–water interactions in otherwise altered catchments (Karr and Schlosser 1978; Ward 1984). Buffer strips obviate, to a remarkable degree, the deterioration of fish habitat conditions often associated with disruption of riparian controls.

Riverine–Floodplain Interactions

Ecological interactions along the lateral dimension reach their apogee in floodplain river systems (Roberts 1972; Gill 1973; Lowe-McConnell 1975; Welcomme 1979; Goulding 1980; Ward 1988). There is a strong correlation between fish catch and the floodplain area of a given river reach (Welcomme 1976).

Waterbodies of the floodplain include side arms, oxbow lakes, marshes, swamps, pools, and the network of tributary streams. During the flood phase these waterbodies merge with one another and with the main river channel. During the dry season many of them are isolated from one another and some dry completely. Locations where the side arms and tributaries breach the natural levees serve as major pathways for lateral migrations of fishes between the river and its floodplain during the periods of rising water at the beginning of the flood season and receding water at the beginning of the dry season. Nutrients that accumulate during the dry period (decomposing vegetation, dung) "rapidly enter into solution during the early stages of flooding, and combined with the river borne silt, support a rapid growth of plants, insects and other forms of aquatic life. This outburst of productivity provides the essential conditions for the reproduction, feeding and growth of the many species of fish which migrate onto the floodplain from the river channel with the rising waters. The flood cycle is vital to the continued survival of these fish species, and any alterations in the intensity or duration of the floods can produce changes in the fish population in following years." (Welcomme 1975, p. 2). Growth, recruitment, and survival of floodplain fishes tend to be maximal during years when gradually increasing water levels are accompanied by a high amplitude flood of long duration (Welcomme 1979; Beumer 1980).

The dependence of floodplain fishes on terrestrial food sources has been best documented in the Amazon basin where water levels during the extended flood season (4–10 months per year) may rise to more than 15 m above dry season levels (Lowe-McConnell 1975; Goulding 1980). This allows fishes access to the inundated forest (Várzea, Igapó) where a variety of species feed on terrestrial arthropods, fruits, seeds, flowers, and leaves that drop into the water.

Man's attempts to develop floodplains invariably involves alterations of the flood regime upon which the integrity of the riverine–floodplain system depends. This results in major disruptions of the lateral transfers of energy and matter between the river channel and the floodplain, and interferes with the lateral (and longitudinal) migrations of fishes. Deforestation reduces the contributions of allochthonous organic matter, increases erosion and siltation, and alters the flood regime. There is an abrupt rise and fall of flood peaks in the absence of the buffering effects of a forested catchment. Destruction of the Amazon alluvial forests (largely intact, but severely threatened; Sioli 1984) would be devastating for the fishes, many of which have evolved morphological and behavior adaptations for exploiting terrestrial food resources (Goulding 1980). Many of the Amazon tributary rivers contain nutrient-poor waters incapable of sustaining an aquatic food base sufficient to support the remarkably diverse and abundant fish fauna (Lowe-McConnell 1975; Sioli 1984). Floodplains are drained for agricultural development and artificial levees are constructed to prevent overspill from the river channels. These alterations alone disrupt floodplain dynamics with severe effects on the fishery (Starret 1972), but dams pose an even more serious threat to riverine–floodplain interactions (Petts 1984).

Typically, flood waters are stored in reservoirs and released slowly, constricting the annual range of discharge downstream, and greatly reducing the area and duration of inundation. In a 145-km reach of the Missouri River, flow regulation that resulted in a 67 % loss of inundated floodplain area, was accompanied by a greater than 80 % decrease in fish catch (Whitley and Campbell 1974). A dam constructed on the Peace River in Canada had a profound effect on the Peace/Athabasca Delta 1100 km downstream (Gill 1973; Townsend 1975; Rosenberg 1986). Prior to regulation, highly productive fish and wildlife habitat conditions were maintained by flooding which maintained plant succession in productive early seral stages. There has been considerable controversy regarding the effectiveness of the ameliorative measures involving weirs that have been undertaken in an attempt to restore at least part of the natural variability lost by regulation (Rosenberg 1986).

Construction of dams on the Kafue River above and below Kafue Flats, a 6 000-km^2 floodplain in Zambia, has imposed a relatively constant flow regime on a system dependent on flooding to maintain high levels of fish productivity (Sheppe 1985). It would be possible to reclaim a major portion of the formerly productive riverine-floodplain system by releasing water from the upstream dam to simulate the seasonal flood. Ideally, a flood regime could be managed to resemble that which occurred naturally during high water years, with enhanced fish production (Dudley 1974).

Damming the Pongolo River severed the connections between the river channel and the floodplain pans, thereby disrupting important aquatic and terrestrial components geared to the seasonal flooding regime (Heeg and Breen 1982). The many flood-dependent fish species resorb gonadal products in the absence of an annual flood and many will not spawn unless terrestrial vegetation is inundated. However, by managing releases from the dam to accommodate spawning migrations and terrestrial–aquatic interactions, it may be possible to sustain a fishery in the regulated riverine-floodplain system (Davies 1979).

Intact riverine–floodplain systems in fact reduce the likelihood of severe flood damage. Regulation of the River Rhine has increased the flood danger; there are plans to allow the river to again inundate portions of the original floodplain to enable the "200-year flood to pass without damage, as was the case before intensive river development" (Friedrich and Müller 1984, p. 278). Improvement of the fishery is certain to result. Much could also be achieved by considering the requirements of key fish species as part of the planning of water releases from dams.

Estuarine reaches are among the most productive waters, but depend on dynamic interactions between freshwater discharge and tidal action to maintain high levels of productivity (Lowe-McConnell 1975; Odum 1971). Tidal creeks, lagoons, salt marches, and mangrove swamps provide major nursery areas for commercial and recreational fishes. For example all the important game and commercial fishes of the North River mangrove swamp in Florida feed on detritivores (mainly crustaceans and fishes) that depend on mangrove leaves for food (Odum and Heald 1975). Diversion or flow regulation results in decreased interactions (e.g. nutrient cycling) between the estuary and the floodplain (Ward et al. 1984). In mesic regions, floodplain areas no longer inundated will revert to terrestrial vegetation. In arid regions, seasonal salt pans may develop.

The Vertical Dimension

Rivers are in intimate contact with groundwater aquifers which are of enormously greater volume than the water contained in river channels. The dynamics of riverine-groundwater interactions, the "vertical" dimension, exert a significant influence on habitat conditions and should be considered in any holistic analysis of river ecosystems (Danielopol 1980; Hynes 1983).

The hyporheic zone, the interstitial habitat within the river bed, is the interface between the free water in the channel and the adjoining groundwater aquifer (Pennak and Ward 1986). This zone is the site of exchange of water and dissolved constituents between groundwater and the river. Hynes (1983) suggests that the hyporheic zone serves as a sink for organic matter and is important to carbon cycling in running waters.

In coarse substrates with silt-free interstices, the hyporheic zone provides habitat for benthic fauna and incubation sites for fish eggs and larvae. A suitable hyporheic zone protects the inhabitants from adverse surface conditions (e.g., drought, flood, temperature extremes), and contains a faunal reserve capable of recolonizing the river bed. Rapid colonization of formerly dry channel segments by fishes may be greatly augmented by the reservoir of benthic animals that survive the drought in hyporheic refuge, thus providing a readily available food resource upon resumption of surface flow.

The value of hyporheic habitat is largely dependent on the presence of sediment-free interstices (Vaux 1962). Excess sediment in the interstitial spaces reduces intragravel flow and oxygen levels, thereby rendering the hyporheic habitat unsuitable for benthos or fish embryos. A study of the impact of logging on salmonid nursery streams in the Alsea River basin of Oregon documented a significant and long-term (7+ years) depression of gravel permeability in a clearcut catchment (Moring 1982). However, permeability values in a partially-logged catchment, with 30 m wide buffer strips along the channel, did not differ significantly from values in a control (unlogged) catchment.

Various activities of man change the height of the groundwater table with sometimes serious ecological consequences. Aggradation in the river immediately upstream from reservoirs results in local elevations in the water table, whereas degradation of the river bed below dams lowers water tables (Simons 1979; Ward 1982; Petts 1984). Even a slight drop in the groundwater table can have a devastating effect on fish survival in floodplain rivers by decreasing the proportion of off-channel habitats that retain water during the dry season (Welcomme 1979).

Groundwater levels play a major role in determining the composition and productivity of riparian and floodplain vegetation (Décamps 1984). Straightening and confining the channel of the Rhine greatly increased current velocity and bed erosion, resulting in a 7 m deepening of the river at Basel (Friedrich and Müller 1984). The concomitant lowering of the water table caused the withering of riparian forests and the drying of backwaters. There are now plans to retain flood waters in polders to recharge the groundwater, raise the water table, and restore the alluvial forest and backwaters along portions of the Rhine.

The Temporal Dimension

Any attempt to understand fully the influence of man on rivers requires a temporal perspective. Man's activities disrupt natural temporal patterns that have structured riverine ecosystems and fish faunas, and that operate over several time-scales. There is an hierarchy of time-scale responses as various processes move toward new equilibrium states following disruption. Because of the hierarchical structure of ecosystems, modifying processes that operate over short time-scales can influence processes occurring over longer time-scales, thereby compounding the effects. A detailed analysis of time-scales is beyond the scope of this paper (see Wiens et al. 1986). Only selected examples of the potential effects of disrupting temporal patterns are presented herein.

Floodplain rivers provide examples of systems dependent on processes occurring over a variety of time-scales (Lowe-McConnell 1975; Welcomme 1975, 1979) that are subject to intervention by man (Ward et al. 1984). The flood dependence of fishes demonstrates this clearly.

Wiens (1977) argues that climatic fluctuations (time-scale in decades) periodically cause selective constraints ("ecological crunches") important in structuring biotic communities. The Sahelian drought is an example of such a constraint for floodplain fishes; species replacements were documented following successive years of flood failure during the recent drought (Welcomme 1979). Less severe year-to-year variations in discharge are reflected in temporal patterns of growth, recruitment, and survival rates of floodplain fishes.

Several major patterns occur with seasonal time-scales. The average duration of floodplain inundation and the timing of the floods within the annual cycle vary from river to river. Fishes tend to move on and off the floodplain with predictable patterns. Lateral migrations by some species are initiated within hours or days of the commencement of flooding. Forms tolerant of low oxygen levels are typically the first to enter (and the last to leave). As water levels decline at the end of the flood season, larger species, predators, and adult fishes move to the river ahead of small species, prey species, and juveniles. Juvenile fishes leave the floodplain in series according to species-specific tolerances of low oxygen conditions. The timing of the lateral migrations of some species is tied to certain phases of the moon, thus superimposing yet another temporal scale.

Longitudinal migrators also show seasonal patterns. Start of flooding initiates migration in some groups, whereas others (e.g., the "piracema" species of S. America) migrate upstream during low water, their arrival at the spawning grounds being synchronized with the arrival of the flood. Most floodplain fishes spawn during the early stages of flooding. Upstream populations may spawn up to a month earlier than downstream populations in large catchments where it requires some time for the flood wave to traverse the entire course of the river. Migration of diadromous fishes may be under severe temporal constraints imposed by sea and river temperatures, resulting in major latitudinal shifts in the periods suitable for movement (Power 1981).

From these few examples of the myriad temporal patterns that may occur, any significant disruption in the timing, duration or magnitude of flooding (even if total discharge remains unaltered) has the potential of greatly modifying the composition and productivity of riverine fishes. Temporal disruptions results in altered predator-prey, competitive, and trophic interactions, and affect fecundity, recruitment, growth, mortality, and ultimately fish yield. The altered environmental conditions may allow hybridization between species whose reproductive periods had been temporally isolated (Zimmerman 1984).

By recognizing the natural time-scales of a river system and accommodating them in management plans, it is often possible to sustain at least a portion of the fishery yet meet other project demands. For example, releasing water from a dam in a pattern that is synchronized with the life cycle requirements of the dominant species will do much to protect the downstream fishery without changing necessarily the annual discharge (Davies 1979; Ward et al. 1984). Petts (1987) applied the time-scale perspective to river regulation, pointing out that different habitat variables respond at different rates as the total river system moves toward a new equilibrium state. Truncation of detrital transport, for example, occurs immediately upon dam closure, whereas physical readjustments of the downstream river channel may continue for decades. Long-term system readjustment must, therefore, also be considered in plans to optimize the fishery within constraints posed by other management objectives.

Conclusions

Rivers are highly interactive systems, the ecological integrity of which depends on events occurring beyond the channel boundaries. The four-dimensional conceptual framework presented in this paper is intended to emphasize the spatio-temporal dynamics of river systems. According to this perspective, man's influence on rivers has been to reduce interactions along spatial pathways and to alter natural time-scales, thereby disrupting the patterns and processes that have structured river ecosystems and riverine fish communities. Rivers in many parts of the world have been straightened, dredged, dammed, and cleared of wood debris; their banks have been reinforced and cleared of vegetation and the floodplains have been drained and developed to suit short-sighted needs. Managed rivers bear little resemblance to their heterogenous aboriginal state characterized by diverse and productive fish faunas. Given the addition of various pollutants, it is remarkable that our highly managed rivers contain any fish fauna. Yet there is hope. The structural and functional attributes of some tropical rivers remain largely intact; it is such systems that clearly demonstrate the remarkable array of adaptive responses that fishes can use to exploit the spatio-temporal patterns characterizing natural river ecosystems.

Civilization is rapidly encroaching on these rivers, however, and their pristine state is severely threatened. Preliminary results from restorative work on rivers such as the Rhine and Thames, cautiously suggest that ameliorative measures can be effective in restoring some of the functional integrity of highly managed rivers, but such improvements may be less true for tropical rivers (Sioli 1984). In many cases at least a portion of the fishery could be accommodated within project design and operation plans. It is our contention that to identify the interactive pathways of critical importance to the fish community of a given river system requires a holistic four-dimensional perspective. Such information would enable the ecological requirements of fishes to be given major consideration early in the project planning stage.

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References

Aleem, A. A. 1972. Effect of river outflow management on marine life. Mar. Biol. 15: 200–208.

Balon, E. K. 1974. Fish production of the drainage area and the influence of ecosystem changes on fish distribution, p. 459–497. *In* E. K. Balon and A. G. Coche [ed.] Lake Kariba: a man-made tropical ecosystem in central Africa. Dr. W. Junk, The Hague.

Banks, J. W. 1969. A review of the literature on the upstream migration of adult salmonids. J. Fish. Biol. 1: 85–136.

Beadle, L. C. 1981. The inland waters of tropical Africa. Longman, London. 475 p.

Benke, A. C., R. L. Henry, III, D. M. Gillespie, and R. J. Hunter. 1985. Importance of snag habitat for animal production in southeastern streams. Fisheries 10: 8–13.

Benson, N. G., and B. C. Cowell. 1967. The environment and plankton density in Missouri River reservoirs, p. 358–373. *In* Reservoir fishery resources symposium. Am. Fish. Soc., Washington, D.C.

Beumer, J. P. 1980. Hydrology and fish diversity of a North Queensland tropical stream. Aust. J. Ecol. 5: 159–186.

Bouvet, Y., E. Pattee, and F. Meggouh. 1985. The contribution of backwaters to the ecology of fish populations in large rivers. Preliminary results on fish migrations within a side arm and from the side arm to the main channel of the Rhone. Verh. Internat. Verein. Limnol. 22: 2576–2580.

Burton, G. W., and E. P. Odum. 1945. The distribution of stream fish in the vicinity of Mountain Lake, Virginia. Ecology 26: 182–194.

Cummins, K. W., G. W. Minshall, J. R. Sedell, C. E. Cushing, and R. C. Peterson. 1984. Stream ecosystem theory. Verh. Internat. Verein. Limnol. 22: 1818–1827.

Davies, B. R. 1979. Stream regulation in Africa: a review, p. 113–142. *In* J. V. Ward and J. A. Stanford [ed.] The ecology of regulated streams. Plenum, New York, NY.

Danielopol, D. L. 1980. The role of the limnologist in ground water studies. Internat. Rev. Ges. Hydrobiol. 65: 777–791.

Décamps, H. 1984. Biology of regulated rivers in France, p. 495–514. *In* A. Lillehammer and S. J. Saltveit [ed.] Regulated rivers. Oslo Univ. Press, Oslo.

Décamps, H., J. Capblanq, H. Casanova, and J. N. Tourenq. 1979. Hydrobiology of some regulated rivers in the southwest of France, p.273–288. *In* J. V. Ward and J. A. Stanford [ed.] The ecology of regulated streams. Plenum, New York, NY.

Dudley, R. G. 1974. Growth of *Tilapia* of the Kafue Floodplain, Zambia: predicted effects of the Kafue Gorge Dam. Trans. Am. Fish. Soc. 103: 281–291.

Friedrich, G., and D. Müller. 1984. Rhine, p. 265–315. *In* B. A. Whitton [ed.] Ecology of European rivers. Blackwell, Oxford.

Gill, D. 1973. Modification of northern alluvial habitats by river development. Can. Geogr. 17: 138–153.

Gosse, J.-P. 1963. Le milieu aquatique et l'écologie des poissons dans la région de Yangambi'. Ann. Mus. R. Afr. Cent. Zool. 116: 113–270.

Goulding, M. 1980. The fishes and the forest. Univ. California Press, Berkeley, CA. 280 p.

Hall, C. A. S. 1972. Migration and metabolism in a temperate stream ecosystem. Ecology 53: 585-604.

Heeg, J., and C. M. Breen. 1982. Man and the Pongolo floodplain. S. Afr. Nat. Sci. Programmes Report No. 56. 117 p.

Hortle, K. G., and P. S. Lake. 1983. Fish of channelized and unchannelized sections of the Bunyip River, Victoria, Aust. J. Mar. Freshwat. Res. 34: 441-450.

Hynes, H. B. N. 1970a. The ecology of running waters. Univ. Toronto Press, Toronto, Ont. 555 p.

1970b. The enrichment of streams, p. 188-196. *In* Eutrophication: causes, consequences, correctives. Nat. Acad. Sci., Washington, D. C.

1975. The stream and its valley. Verh. Internat. Verein. Limnol. 19: 1-15.

1983. Groundwater and stream ecology. Hydrobiologia 100: 93-99.

Illies, J., and L. Botosaneanu. 1963. Problèmes et méthodes de la classification et de la zonation écologique des eaux courantes, considérées surtout du point de vue faunistique. Mitt. Internat. Verein. Limnol. 12: 1-57.

Karr, J. R., and I. J. Schlosser. 1978. Water resources and the land-water interface. Science 201: 229-234.

Lowe-McConnell, R. H. 1975. Fish communities in tropical freshwaters. Longman, London. 337 p.

Moring, J. R. 1982. Decrease in stream gravel permeability after clear-cut logging: an indication of intragravel conditions for developing salmonid eggs and alevins. Hydrobiologia 88: 295-298.

Mosley, M. P. 1983. Variability of water temperatures in the braided Ashley and Rakaia Rivers. N. Z. J. Mar. Freshwat. Res. 17: 331-342.

Mundie, J. H. 1979. The regulated stream and salmon management, p. 307-320. *In* J. V. Ward and J. A. Stanford [ed.] The ecology of regulated streams. Plenum, New York, NY.

Nikolsky, G. V. 1963. The ecology of fishes. Acad. Press, London. 352 p.

Odum, E. P. 1971. Fundamentals of ecology. Saunders, Philadelphia, PA. 574 p.

Odum, W. E., and E. J. Heald. 1975. Mangrove forests and aquatic productivity, p. 129-136. *In* A. D. Hasler [ed.] Coupling of land and water systems. Springer-Verlag, New York, NY.

Pennak, R. W., and J. V. Ward. 1986. Interstitial faunal communities of the hyporheic and adjacent groundwater biotopes of a Colordo mountain stream. Arch. Hydrobiol. Suppl. (Monogr. Beiträge) 74: 356-396.

Petts, G. E. 1984. Impounded rivers. Wiley, Chichester. 326 p.

1987. Time-scales for ecological change in regulated rivers, p. 257-266. *In* J. F. Craig and J. B. Kemper [ed.] Advances in regulated streams ecology. Plenum, New York, NY.

Power, G. 1981. Stock characteristics and catches of Atlantic salmon (*Salmo salar*) in Quebec, and Newfoundland and Labrador in relation to environmental variables. Can. J. Fish. Aquat. Sci. 38: 1601-1611.

Rasmussen, J. L. 1983. A summary of known navigation effects and a priority list of data gaps for the biological effects of navigation on the upper Mississippi River. U.S. Army Corps of Engineers, Rock Island, Illinois. 96 p.

Roberts, T. R. 1972. Ecology of fishes in the Amazon and Congo basins. Bull. Mus. Compar. Zool. 143: 117-147.

Rosenberg, D. M. 1986. Resources and development of the Mackenzie system, p. 519-540. *In* B. R. Davies and K. F. Walker [ed.] The ecology of river systems. Dr. W. Junk, Dordrecht, The Netherlands.

Roux, A. L. 1984. The impact of emptying and cleaning reservoirs on the physico-chemical and biological water quality of the Rhone downstream of the dams, p. 61-70. *In* A. Lillehammer and S. J. Saltveit[ed.] Regulated rivers. Oslo Univ. Press, Oslo.

Rzóska, J. [ed.] 1976. The Nile, biology of an ancient river. Dr. W. Junk, The Hague. 417 p.

Sedell, J. R. and J. L. Froggatt. 1984. Importance of streamside forests to large rivers: the isolation of the Willamette River, Oregon, U.S.A., from its floodplain by snagging and streamside forest removal. Verh. Internat. Verein. Limnol. 22: 1828-1834.

Sheppe, W. A. 1985. Effects of human activities on Zambia's Kafue Flats ecosystem. Environ. Conserv. 12: 49-57.

Simons, D. B. 1979. Effect of stream regulation on channel morphology, p. 95-111. *In* J. V. Ward and J. A. Stanford [ed.] The ecology of regulated streams. Plenum, New York, NY.

Sioli, H. [ed.] 1984. The Amazon. Dr. W. Junk, Dordrecht, The Netherlands. 763 p.

Stanford, J. A. and J. V. Ward. 1986a. Fishes of the Colorado system, p. 385-402. *In* B. R. Davies and K. F. Walker [ed.] The ecology of river systems. Dr. W. Junk, Dordrecht, The Netherlands.

1986b. The Colorado River system, p. 353-374. *In* B. R. Davies and K. F. Walker [ed.] The ecology of river systems. Dr. W. Junk, Dordrecht, The Netherlands.

Starrett, W. C. 1972. Man and the Illinois River, p. 131-169. *In* R. T. Oglesby, C. A. Carlson, and J. A. McCann [ed.] River ecology and man. Acad. Press, New York, NY.

Talling, J. F., and J. Rzóska. 1967. The development of plankton in relation to the hydrological regime in the Blue Nile. J. Ecol. 55: 637-662.

Townsend, G. H. 1975. Impact of the Bennett Dam on the Peace-Athabasca delta. J. Fish. Res. Board Can. 32: 171-176.

Valdez, R. A., and E. J. Wick. 1983. Natural versus manmade backwaters as native fish habitat, p. 519-536. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publ., Ann Arbor, Michigan.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130-137.

Vaux, W. G. 1962. Interchange of stream and intergravel water in a salmon spawning riffle. Spec. Publ. U.S. Fish Wildl. Serv. 405: 1-11.

Walker, K. F. 1979. Regulated streams in Australia: The Murray-Darling River System, p. 143-163. *In* J. V. Ward and J. A. Stanford [ed.] The Ecology of Regulated Streams. Plenum, New York, NY.

1985. A review of the ecological effects of river regulation in Australia. Hydrobiologia 125: 111-129.

Ward, J. V. 1982. Ecological aspects of stream regulation: responses in downstream lotic reaches. Wat. Poll. Mgmt. Reviews (New Delhi) 2: 1-26.

1984. Ecological perspectives in the management of aquatic insect habitat, p. 558-577. *In* V. H. Resh and D. M. Rosenberg [ed.] The ecology of aquatic insects. Praeger, New York, NY.

1985. Thermal characteristics of running waters. Hydrobiologia 125: 31-46.

1986. Altitudinal zonation in a Rocky Mountain stream. Arch. Hydrobiol. Suppl. (Monogr. Beiträge) 74: 133-199.

1988. Riverine-wetland interactions. *In* R. R. Sharitz and J. W. Gibbons [ed.] Freshwater wetlands and wildlife. U.S. Dep. Energy, Oak Ridge, TN. (in press)

Ward, J. V., B. R. Davies, C. M. Breen, J. A. Cambray, F. M. Chutter, J. A. Day, F. C. de Moor, J. Heeg, J. H. O'Keeffe, and K.F. Walker. 1984. Stream regulation, p. 32-63. *In* R. C. Hart and B. R. Allanson [ed.] Limnological criteria for management of water quality in the Southern Hemisphere. S. Afr. Nat. Sci. Programmes Report No. 93.

WARD, J. V. AND J. A. STANFORD. 1983. The serial discontinuity concept of lotic ecosystrems, p. 29–42. *In* T. D. Fontaine and S. M. Bartell [ed.] Dynamics of lotic ecosystems. Ann Arbor Science Publ., Ann Arbor, MI.

WELCOMME, R. L. 1975. The fisheries ecology of African floodplains. FAO, Rome. 51 p.

1976. Some general and theoretical considerations on the fish yield of African rivers. J. Fish. Biol. 8: 351–364.

1979. Fisheries ecology of floodplain rivers. Longman, London. 317 p.

WHITLEY, J. R., AND R. S. CAMPBELL. 1974.Some aspects of water quality and biology of the Missouri River. Trans. Missouri Acad. Sci. 8: 60–72.

WIENS, J. 1977. On competition and variable environments. Am. Sci. 65: 590–597.

WIENS, J., J. ADDICOTT, T. J. CASE, AND J. DIAMOND. 1986. Overview: the importance of spatial and temporal scale in ecological investigations, p. 145–153. *In* J. Diamond and T. J. Case [ed.] Community Ecology. Harper and Row, New York, NY.

ZALUMI, S. G. 1970. The fish fauna of the lower reaches of the Dnieper: its present composition and some features of its formation under conditions of regulated and reduced river discharge. J. Ichthyol. 10: 587–596.

ZIMMERMAN, E. G. 1984. Genetic and physiological correlates in fish adapted to regulated streams, p. 273–292. *In* A. Lillehammer and S. J. Saltveit [ed.] Regulated rivers. Univ. Oslo Press, Oslo.

Large Rivers are More than Flowing Lakes: a Comparative Review[1]

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Abstract

RYDER, R. A., AND J. PESENDORFER. 1989. Large rivers are more than flowing lakes: a comparative review, p. 65–85. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish Aquat. Sci. 106.

The tendency to consider rivers as a subset of lakes is tempting, particularly for the purpose of science transfer. However, real qualitative differences exist that make such transfer impractical, unless the differences are first accounted for. Differences between rivers and lakes may be aptly expressed in terms of six dichotomies, namely: space-time orientation; horizontal or vertical stratification; exogenous or endogenous environmental influence; allochthonous or autochthonous sources of energy and nutrients; relative levels of abiotic and biotic effects; and proportional distribution of autotrophic and heterotrophic production. Other important qualitative differences relate to morphology, hydrodynamics, temperature, chemistry, and biota. Rivers possess certain ecological peculiarities not found in lakes, or at least that are less significant there. These include the boundary layer, nutrient spiralling, the hyporheic zone, and various reset events.

Résumé

RYDER, R. A., AND J. PESENDORFER. 1989. Large rivers are more than flowing lakes: a comparative review, p. 65–85. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

La classification des rivières comme un sous-ensemble des lacs constitue une option fort attrayante surtout pour ce qui est du transfert scientifique. Toutefois, il existe des différences qualitatives réelles qui rendent un tel transfert irréalisable à moins de justifier ces différences en premier lieu. Les différences entre les lacs et les rivières peuvent être exprimées en termes de six dichotomies, soit: orientation spatio-temporelle, stratification horizontale ou verticale, influence environnementale exogène ou endogène, sources d'énergie et de bioéléments allochtones ou autochtones, niveaux relatifs d'incidences abiotiques et biotiques, et répartition proportionnelle de la production autotrophe et hétérotrophe. D'autres importantes différences qualitatives se rapportent à la morphologie, à l'hydrodynamique, à la température, à la composition chimique et au biote. Les rivières possèdent des caractéristiques écologiques absentes des lacs ou au moins de moindre importantes. Celles-ci comprennent la couche limite, la spiralisation des bioéléments, la zone hyporhéique et les divers événements de recalage.

Because of the inordinately high ratio of lakes to large rivers in the northern hemisphere as compared to the situation in the tropics (Fernando 1980), advancement in the development of techniques applicable to the study of rivers has suffered. This disproportionate emphasis on lakes is not unique to any particular jurisdiction or country. For example, Huet (1959) noted a similar inequity between research in standing freshwaters such as lakes, ponds, and marshes, as compared with running waters in Western Europe. Apparently, pristine river systems have been particularly neglected worldwide (Statzner and Higler 1985). Welcomme (1979) also observed an imbalance between the available font of information existing for lakes as opposed to rivers, and suggested that only recently have comparable efforts been made in the area of river fisheries in some parts of the world. Perhaps this inequitable treatment of rivers stems from the fact that on a volumetric basis they constitute only 0.004 % of the world's fresh waters (calculated from data presented in Vallentyne 1972).

Ricker (1934) with remarkable prescience, suggested the possibility of extending to streams generally, the systematic ecological treatment already applied to lakes. The comparative approach among lakes, reservoirs and rivers has produced both interesting and informative ecological insights (e.g. Ryder 1978a; Regier and Henderson 1980). We intend to extend these insights to a comparison and contrast of large lakes and rivers of the world. We attempt this exercise within the context of the "River Continuum Concept" (Vannote et al. 1980; Minshall et al. 1985; Sedell et al. 1989) and one of its logical extensions, the "Land–Stream–Bay–Lake–Continuum" (Francis et al. 1985). Neither our topics (morphology, hydrodynamics, temperature, chemistry, trophodynamics, biota), nor our treatment, is intended to be exhaustive, but rather, to serve as a general entry into important facets of river ecology, and particularly, to provide an ecological foundation for future studies of fish production.

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Distinguishing Features

Rivers and lakes have many physical, chemical, and ecological features that may be readily compared or contrasted. We have selected some of the most prominent attributes of both lotic and lentic systems, in order to demonstrate the fundamental differences or commonalities. This compare-and-contrast exercise focuses sequentially on morphology, hydrodynamics, temperature, chemistry and ecology. Much of the information presented in the text has been summarized in tabular and graphic form for ready comprehension. The perspective portrayed is, of necessity, that based upon the authors' previous experience, and is intended to provoke further insights into river ecology. Other perspectives derived from the same set of information may be equally valid.

Morphology

Many morphological characteristics of rivers distinguish them from lakes (Table 1), although the typical river system embodies both lotic and lentic features (e.g. Moss 1980). River habitat as characterized by morphometry, is a dynamic, often ephemeral phenomenon, which is typified by seasonal and spatial changes (Leopold et al. 1964). Hynes (1970) suggested that a network of variables (discharge, width, depth, rate of flow, substrate resistance, and sediment transport) interact, undergoing constant adjustment, to achieve the existing river channel characteristics. The physical and hydrobiological features of a river are strongly interrelated; for example, swiftly flowing water is typically associated with a stony substrate (Smith 1980), high elevations, and a propensity to frequent, fierce storm flows (Haslam 1978). As a result, the lotic ecosystem approaches a state of conservative dynamic equilibrium.

TABLE 1. A comparison of relative morphological attributes, primarily for north-temperate rivers and lakes.

Attribute	Rivers	Lakes
Channel or basin contours	Changes spatially	Constant
Erosion/deposition ratio	Decreases downstream	Decreases from near-shore littoral to greater depths
Shoreline erosion	Extensive, induced by water currents	Localized, induced by wind-driven waves
Mean particle size	Decreases downstream	Decreases with depth
Number of substrate types	Increases downstream	Determined by geomorphology and wave action
Distribution of substrate	Determined by water current; gravity driven	Determined by wind-induced currents
Mean depth	Low	High
Depth gradient	Increases from headwaters to mouth	Deepest remote from shore
Shape	Long, meandering, linear	Short, ovoid
Breadth/shoreline length ratio	Low	High
Watershed/surface area ratio	High	Low
Turbidity	High	Low
Ice formations	Transitory	Persistent
Ice scouring effects	Robust, extensive	Localized to windward, near-shore littoral

Data were derived in part from the following sources: Hynes 1970; Vannote et al. 1980; Statzner and Higler 1985.

The morphological characteristics of a river change as its water moves from the source to the mouth; for example, the topography assumes a lower profile and the channel gradient generally decreases (Haslam 1978). The gradient from headwaters to the mid-reaches and thence to the mouth, has been described as a "spectrum of differentially variable habitats" (Minshall et al. 1985). The gradient of a river dictates the direction and rate of flow; thus, it determines the course of a river. In addition, slope or gradient is usually indicative of the type of fish fauna present (Huet 1946, 1949; Hocutt and Stauffer 1975), as well as other taxa (Hynes 1970; Cummins and Spengler 1978). The channel generally widens and deepens in a downstream direction; however, channel width increases more rapidly than depth (Hynes 1970; Beaumont 1975; Haslam 1978). The ecological significance implicit therein is that within any given biogeographical area, rivers of comparable breadth, depth and slope, exhibit faunal characteristics of great similitude (e.g. Huet 1959).

On the other hand, the basin morphology of lakes remains relatively stable, except for moderately small and localized effects caused by wind-induced waves and subsequent sedimentation (Table 1).

Rivers integrate erosional and depositional habitats, the former typically occurring in sections where rapid flow prevails, often in the narrow, upper reaches, while deposition of silt and detritus occurs in regions of slow current (Shelford 1914; Shelford and Eddy 1929; Moon 1939; Statzner and Higler 1985). Banks of rivers may erode, shift, or form levees on one or both sides of the river, as has happened, for example, in some of the large rivers of the Hudson Bay lowlands. Material input and transport capacity must be in dynamic equilibrium if the stream bed is neither to erode, nor to accumulate debris or silt (Statzner and Higler 1985).

Overall, lakes are more stable physically, and, in general, their shorelines are eroded more slowly than are the banks of rivers. While the causative factors in natural river bank erosion are primarily water current and changing water levels, erosion of lake shores is largely due to wind-induced waves (Table 1).

In the middle reaches of rivers, the gradient generally decreases to intermediate levels (Patrick 1972; Smith 1980). However, the current velocity may be slightly increased (Hynes 1970; Patrick 1972), and the silt load suspended by the water becomes greater (Patrick 1972). This stream region, transitional between erosional upper reaches and depositional lower reaches (Statzner and Higler 1985), is characterized by larger meanders than in the upstream reaches (Patrick 1972; Smith 1980). In the lower stream reaches the gradient flattens markedly and sedimentation of suspended materials increases.

Depth variability, so characteristic of rivers, indirectly influences the various biotic components. When compared with lakes, the mean depth in rivers may be described as relatively shallow throughout. Deep and shallow areas are usually represented by alternating pools and riffles (Hynes 1970).

Lakes, on the other hand, have relatively high mean depths (Table 1). Shallow areas of lakes generally are found adjacent to shore, where extensive littoral formations may occur. Outer waters remote from shore are usually deepest.

Seen from above, a river is a long, meandering, ribbon-like water body, unlike the relatively short, ovoid shape of a typical lake. Thus, the breadth/shoreline length ratio of lakes far surpasses that of rivers. On the other hand, the watershed/surface area ratio of rivers exceeds that of virtually all lakes and accounts, in part, for the inordinately great effect of exogenous processes on rivers (Table 1).

The two types of water bodies converge, however, in the sense that the most ecologically diverse lotic and lentic ecosystems occur concomitant to maximum aquatic edge or ecotone. This is likely due to the fact that ecological diversity, in terms of species numbers, is often related to environmental heterogeneity (MacArthur 1972). Meanders, for example, are physically complex, indicative both of increasing aquatic edge and greater depth; hence, they create ecological diversity in rivers (Hynes 1970), while an irregular shoreline is conducive to ecological diversity in lakes (Moyle and Cech 1982). Large water bodies, be they rivers or lakes, are usually more complex environmentally than are small water bodies, due to scale factors alone. A measure of available ecotone in rivers, similar to the shore development factor for lakes (Hutchinson 1957), would be a useful adjunct to stream survey methodologies.

An awareness of the transitional changes from the headwaters to the downstream waters, plus the fact that many stream characteristics are similar from one stream to the next, have necessitated a general classification of the various stream reaches (Winger 1981). In this classification, an assigned number indicates the "stream order" (Strahler 1957 as modified from Horton 1945), which aptly characterizes the morphology and fish populations of a given reach (Platts 1979; Vannote 1980).

The lotic environment is typically more turbid than the lentic environment (Table 1). Turbidity levels vary from headwaters to mouth, from river to river, and temporally within any stream (Winger 1981). The muddy-bottomed, downstream areas where the mean particle size of the substrate decreases (Hynes 1970; Smith 1980), are generally the most turbid (Moyle and Cech 1982) except for glacial streams. Turbidity at high levels may represent an environmental stress (Wallen 1951). The consequences of excessive turbidity are as follows: (1) reduced light penetration, and therefore, reduced photosynthesis; (2) altered water chemistry; (3) altered physical habitat; (4) injuries to biota (Cairns 1968; Iwamoto et al. 1978); (5) reduction in standing stocks of benthos; and (6) hindered reaeration (Cordone and Kelly 1961). Turbidity is likely to be more critical in rivers than in lakes (Table 1) because of the vulnerability of the former habitat to rapid changes in water levels and bank undercutting.

The consequences of ice formation and movement likely affect the morphology of rivers more severely than is the case with lakes. These effects extend to river biota in the form of physiological traumata. The ice formed on rivers rarely persists for the entire winter in the southern part of the north-temperate zone, unlike lakes where surface ice tends to endure from fall to spring, and persists longer than river ice at the same latitude. The various types of ice formed on rivers, such as "frazil" and "anchor" ice (Hynes 1970), undergo a continuous formation/breakdown process, with the end result being the prevalence of more open-water areas during winter in rivers than in lakes at the same latitude (Table 1).

River beds are susceptible to far greater levels of ice scouring than are most substrates of lakes except for their shallow eulittoral zones. Many rivers will freeze to the substrate, at least in the near-shore areas.

Hydrodynamics

Lotic ecosystems are characterized by continuously moving, unidirectional flows (except where tidally influenced), which tend to transport matter downstream, and by fluctuations in the annual water yield (Table 2; Benfield 1981; Speaker et al. 1984). The current and its debris contour the morphology of a river channel; the velocity determines the rate of silt deposition and the substrate type, and influences the biota profoundly (Smith 1980). Characteristics of lotic water columns, and thus velocities, are determined by the following controlling factors: (1) the channel form; (2) the channel gradient; (3) the volume of water in the channel; (4) the river bank; and (5) the substratum type (Platts et al. 1983). This tightly-knit complex of interacting variables fluctuates constantly, and acts in concert to determine the varying stream velocities. The velocity of the water column may, therefore, increase over the length of a river as the channel widens, or it may remain stable (Leopold 1953; Hynes 1970). In any case, width and depth generally

TABLE 2. A comparison of certain hydrodynamic properties of rivers and lakes found primarily in the north temperate region.

Attribute	Rivers	Lakes
Flow characteristics	Unidirectional, horizontal	Three-dimensional
Current	Gravitational movement, decreases vertically	Wind-induced, convectional
Flow diversions	Common, habitat implications	Rare
Langmuir vortices	Rare	Frequent
Taches d'huiles	Rare	Common
Chemical stratification	Estuarine reaches	Meromictic lakes
Water level fluctuations	Flooding	Minor variations
Flooding effects on biota	Traumatic; reset event	Diminished

Data were derived, in part, from the following sources: Hynes 1970; Ryck 1975; Speaker et al. 1984.

increase more rapidly than velocity in a downstream direction (Beaumont 1975). The current decreases from the surface to the bottom of the river, where a boundary layer (1–3 mm thick) of very slow current exists (Ambühl 1961).

Structural factors may change stream velocities, divert the direction of flow, and hence, alter existing stream habitat conditions. Several examples of structures affecting the stream ecosystem throughflow are riffles, falls, rapids, debris, beaver dams, and ice.

Patterns of flow are also determined by slope and volume of flow, which in turn determine pool/riffle ratios. The more resistant reaches (e.g. riffle areas) are characterized by a steeper slope than are the smooth-flowing areas such as pools (Hynes 1970). Consequently, as the slope decreases and the rate of flow increases, pools and smooth-flowing areas become progressively more prevalent following the turbulent headwater reaches, until the water eventually flows evenly (Neel 1951).

Lake ecosystems are subject to three-dimensional water flows in most cases (Table 2). The currents are largely wind-induced, and these have the potential to affect the distribution of suspended particulate matter and thereby influence sedimentation rates. However, unidirectional flow patterns may arise in localized areas, as a consequence of thermal bars, resulting in coastal currents or currents generated by influent streams (Wetzel 1975). Furthermore, a slight one-way current may exist in lakes between inlets and outlets (Moyle and Cech 1982). Unlike rivers, water movement in lakes is not usually gravitationally induced; however, convectional (gravitational) water movements during spring or fall overturn do occur in dimictic lakes, and remain unique features of them (Table 2). Furthermore, shoals comprised of debris and other lake structures do not form major obstructions to the flow, as a rule. Debris, however, may be entrained within Langmuir vortices, which are common characterictics of lakes, but which are only seldom seen in rivers. "Taches d'huile" or oil slicks, are another feature which are probably unique to lakes (Hutchinson 1957). These are due, usually, to the presence of a plankton-generated oil film on the surface of the water which impedes wind-induced water currents.

A considerable degree of density stratification may occur in the estuarial areas of rivers, where fresh water flows over the incoming salt water (Patrick 1972). Within this context, river estuaries can be likened to a chemically stratified meromictic lake, with the highest salinity concentrations (marine intrusions) occurring on the bottom (Table 2).

In rivers, flooding affects every biotic component (Ryck 1975), whereas the effects in lakes may be substantially less. Odum (1971) suggested that lotic environments are open systems due to flooding, since an exchange of water, sediments, organic matter, and nutrients takes place between stream and watershed when the water impinges upon the land/water interface. Floods may scour aquatic vegetation from the stream bed and determine, at least in part, the depositional volumes of silt and organic debris downstream. In lakes, water level fluctuations are much less dramatic and potentially less devastating (Table 2).

Temperature

Temperatures fluctuate much more rapidly in rivers than in lakes (Table 3), but variations occur within a tight range (Hynes 1970). In fact, both diel and annual thermal periodicity patterns exist for rivers in a seasonal climate (Ward 1985). The diel minima occur in early morning, while the maxima are reached in mid or late afternoon, occurring later with increasing distance downstream in the northern hemisphere (Schmitz 1954; Yakuma 1960). Rates of temperature change may be as high as 3 °C per hour (Brown 1969), while diurnal temperature variations of up to 6 °C may occur due to the absorption of solar radiation or the subsequent release of heat from the water to the atmosphere (Hynes 1970).

Except in great depths of 15 m or more, the main river channel generally remains thermally unstratified due to the mixing action which is achieved by the current (Hynes 1970; Welcomme 1979). Dimictic lakes, however, do possess vertical thermal stratification, which is seasonally dynamic. The epilimnion, the freely circulating surface layer, is the warmest layer and fluctuates along a small temperature gradient (Smith 1980), always at dynamic equilibrium with the air temperature (McCombie 1959). Below this, the metalimnion or thermocline declines rapidly in temperature (at least 1 °C for each metre of depth by definition; Welch 1952), but the deepest layer, the hypolimnion, decreases in temperature much more slowly, usually until maximum density is reached at 4 °C in north-temperate lakes. Usually lakes take longer to reach their maximum summer temperatures, as spring overturn must precede the ultimate warming of surface waters in north-temperate,

TABLE 3. A comparison of thermal properties of rivers and lakes found primarily in the north-temperate region.

Attribute	Rivers	Lakes
Temperature variation	Fluctuates rapidly	Stable
Density stratification	No	Yes
Temperature maxima	Downstream	Epilimnion
Air temperature effects	Considerable	Diminished
Air-water equilibrium temperature	Water temperature lags behind air temperature except in downstream reaches	Equal to water temperature of epilimnion surface
Temperature cline (summer)	Cold headwaters, warm downstream areas	Cold hypolimnion, warm epilimnion
Groundwater/surface drainage ratio (summer)	High ratio decreases temperature; low ratio increases temperature	Significant only in seepage lakes; effect same as in rivers
Tributary effects on temperature	Considerable	Diminished and localized
Shading effects on temperature	Considerable; create thermal stability	Diminished

Data were derived, in part, from the following sources: McCombie 1959; Hynes 1970; Welcomme 1979; Smith 1980; Ward 1985.

dimictic lakes. In general, then, temperatures of these lakes are more stable than river temperatures (Table 3), especially in the subsurface layers during the two annual periods of density stratification.

A complex of regional climatic factors act in concert to determine the river's temperature regime. Ward (1985) suggested that air temperature is the most important of these. He noted that air temperature influences groundwater temperature and equilibrium temperature (water temperature at which net heat exchange with the atmosphere is zero). Stream temperatures generally follow, but lag behind the air temperature and therefore, the equilibrium temperature (Ward 1985). Downstream, however, less shading by vegetation exists, and greater surface area is exposed to solar radiation, causing temperatures to increase until a dynamic equilibrium with the air temperature is reached (Hynes 1970).

The source of the water in a river is another noteworthy hydrobiological variable affecting temperature (Ward 1985). If the stream is spring-fed, the headwaters and upper reaches are generally cool in summer and warm in winter because the water originates underground (Hynes 1970; Patrick 1972; Ward 1985). The temperatures in the upper reaches of spring-fed rivers remain relatively constant throughout the year, as well as on a daily basis, in comparison to those streams which are fed primarily by surface drainage (Hynes 1970; Patrick 1972; Ward 1985). The relative proportion of groundwater/surface drainage will tend to influence water temperatures. In the spring, snowmelt may either decrease or increase stream temperatures, depending on the type and distance of surface conditions traversed. Similarly, if a river is fed by way of a lake outlet, the ensuing river temperature may reflect, in part, the water temperature of the parent water body.

Tributaries have potentially profound influences on a stream's water temperature (Table 3). They may have higher summer temperatures than the main channel if they are smaller or exposed to more solar radiation (Ward 1985). On the other hand, heavily vegetated stream banks or a greater influx of spring water, tend to have a cooling effect in summer.

In lakes, the role of tributaries in determining temperature is less significant and usually localized. The relative volume of inflowing tributary water is often negligible compared to the great volume within a lake, which in itself, greatly enhances the system's temperature buffering capacity. On the same note, springs do not evoke the same temperature effects in drainage lakes as in rivers, due once more to the greater volumetric buffering capacity of lakes.

Stream sections which are shaded by fringing vegetation (i.e. trees, shrubs) or steep, or overhung banks, may be cooler than stream reaches which have large areas exposed to direct sunlight (Welcomme 1979; Smith 1980). These shaded stream areas, which are often headwater reaches, also tend to exhibit a high degree of thermal stability (Welcomme 1979). According to Barton et al. (1985), unshaded streams reach their maximum daily temperatures earlier in the day than shaded streams; however, the two stream types achieve minima at night during comparable time periods.

In lakes, because the ratio of shoreline to surface area is relatively smaller than in rivers, the shading effect of vegetation on the total water body is relatively slight, or even insignificant (Table 3).

Floating vegetation may promote the attainment of very high temperatures in rivers (Welcomme 1979, 1985); presumably, flood plain rivers and high order reaches, with their associated slow current and lentic characteristics, are most conducive to such accumulations of floating vegetation. If the vegetation is of considerable thickness, evaporation is restricted, sunlight is absorbed, and wind and wave action are reduced; hence, temperature increases may be dramatic. For example, Welcomme (1979) noted temperatures of up to 40°C in an African oxbow lake covered with water ferns (*Salvinia auriculatus*).

Suspended silt also absorbs heat energy, thus increasing temperatures in turbid rivers where large silt loads are being transported (Ellis 1936; Reid 1961). In some areas, however, warmer waters may carry a reduced silt load, flow somewhat faster, and have a thinner boundary layer.

Chemical Characteristics

A singular feature of lotic ecosystems is their chemical homogeneity (Table 4), caused by turbulence throughout the water column (Winger 1981). However, the concentrations of various chemicals dissolved in rivers vary greatly according to region, and they reflect such factors as the climate, physiography, geology and biota (e.g. Hynes 1970; Welcomme 1979). More specifically, factors influencing the surface water chemistry include precipitation, nature of the

TABLE 4. A comparison of some key chemical characteristics of water, especially as applied to north-temperate rivers and lakes.

Attribute	Rivers	Lakes
Vertical chemical profile	Homogeneous	Stratified
Diel periodicity for various chemicals	Yes	Yes, at interfaces
Dissolved gases in dynamic equilibrium with atmospheric gases	Yes	No
Oxygen content	Usually high	Variable
Oxygen uptake ability at water surface	High	Variable
Diurnal variation of dissolved O_2	Yes; dependent upon photosynthesis and respiration rates, and decomposition	Not significant
Phosphorous	Variable, headwaters to mouth	High in spring and at overturns
Total dissolved solids	Increase downstream	Temporal cycle
Turbidity	High; varies among rivers and spatially	Low; varies among lakes and temporally

Data were derived, in part, from the following sources: Hynes 1970; Smith 1980; Winger 1981.

bedrock, and the dynamics of the evaporation–crystallization process (Gibbs 1970). The "Gaia" hypothesis (Lovelock 1979) invokes biotic factors as controllers of atmospheric conditions through feedback, which provides desirable biospheric conditions. As an ultimate consequence, chemical stoichiometry in rivers may be under the regulation of the biosphere through biogeochemical homeostasis (e.g. Holling 1985).

Winger (1981) categorized stream chemicals into 5 classes of compounds: (1) dissolved inorganic ions and compounds; (2) particulate inorganic compounds; (3) dissolved organic compounds; (4) particulate organic material; and (5) dissolved gases. The dissolved gases in lotic ecosystems, such as oxygen, nitrogen and carbon dioxide, are generally in dynamic equilibrium with the atmosphere (Hynes 1970).

Dissolved oxygen levels in rivers are rarely inadequate for the respiration of biota and putrefaction processes (Winger 1981); in fact, in small, turbulent streams, the oxygen content may transcend the saturation point during certain seasons (Hynes 1970; Smith 1980). The two major sources of dissolved oxygen in streams are the water–air interface zone and photosynthesizing plants. In the first instance, turbulent waters have greater surface area contact with the atmosphere, thus, oxygen uptake is facilitated (Smith 1980). Hynes (1970) noted that the amount of air uptake varies approximately with the velocity, and that air can comprise up to 60 % of the water volume.

Variations in the oxygen content of rivers do occur, both diurnally and seasonally. The diurnal variations are largely dependent upon the rates of photosynthesis and respiration of the stream biota (Hynes 1970). Seasonal variations may take place due to: (1) leaf inputs in the fall, which increase oxygen demand; (2) seasonal photosynthesis peaks and declines; (3) winter ice-cover on rivers, which serves to decrease oxygen levels; and (4) high discharge situations which tend to reduce the oxygen content (Hynes 1970). Dissolved oxygen and carbon dioxide are generally inversely related, because of photosynthetic and respiratory rates of stream organisms (Hynes 1970) as well as the decomposition of organic matter (Winger 1981).

Dissolved oxygen in lakes also originates from both the atmosphere and from photosynthetic activity of plants. Under certain circumstances, the latter activity may result in supersaturation levels or alternatively, result in a net oxygen deficit (e.g. Hutchinson 1957). The oxygen content of lake water is generally lower than that of lotic waters (Smith 1980). He suggests that oxygen levels, which are usually highest in the surface areas, decrease with depth. Oxygen depletion in lakes, as in rivers, may be severe under the ice.

Total dissolved solids (TDS) tend to increase in the downstream reaches of streams (Winger 1981). The major cations contributing to TDS in rivers, in descending order of concentration, are calcium, magnesium, sodium and potassium (Reid 1961). Calcareous rivers are generally the most productive (Hynes 1970), which is true also of calcareous lakes. Silicon is another element essential to the survival of river biota. The levels may fluctuate between 2 and 9 mg/L, since SiO_2 is depleted as diatoms replace the lost halves of their shells subsequent to cell division (Müeller 1974).

Phosphorous is the element which is most often a limiting factor in primary production of freshwater ecosystems (Hutchinson 1957; Schindler 1977). Therefore, its concentration, spatial distribution and temporal regime are important. The major allochthonous sources of phosphorous in both streams and lakes are rainfall and the land surface of the immediate watershed (Hutchinson 1957; Hynes 1970). However, in lakes, a larger proportion of available phosphorous may be of autochthonous derivation than in rivers, the latter being more strongly influenced by the abiotic environment (Sanders 1972). While phosphorous concentrations may vary in time and space in both rivers and lakes (Table 4), the largest variations for rivers would seem to be spatially organized, from headwaters to mouth, while for lakes, temporal variability is usually greatest. Both rivers and lakes in the north-temperate zone usually reach annual high phosphorus concentrations during the spring runoff period (Table 4; Dillon and Rigler 1975).

Trophodynamics

Rivers have been described as continua, or gradients (Cushing et al. 1983), in which "ecosystem level processes in downstream areas are linked to those in upstream areas" (Minshall et al. 1985). This implies a dynamic, longitudinally-linked system, in which a conspicuous transition occurs from headwaters to downstream reaches. Many of the headwater regions are typically forested; hence, erosion is minimal and the water is clear (Patrick 1972). As a result, photosynthesis may occur across the width of the stream (Patrick 1982); presumably, this is true only in wide, unshaded stretches of headwater streams. Alternatively, if the headwaters are narrow, the extensive shading of riparian vegetation may not only limit photosynthesis considerably, but also supply large amounts of allochthonous matter in the form of leaf fall (Vannote et al. 1980). Certainly, allochthonous detrital inputs have been universally touted as being the primary energy source in lotic ecosystems (Table 5; Hynes 1963, 1975; Cummins 1975; Cummins and Klug 1979; Welcomme 1979; Moss 1980). Similarly, the importance of terrestrial vegetation and adjacent land areas in influencing stream trophodymanics is currently well recognized (e.g. Cummins et al. 1984; Minshall et al. 1985). The organic carbon supply in rivers is furnished primarily by allochthonous organic material (Moss 1980); however, it is usually complemented by significant amounts of aquatic plant production, both spatially and seasonally (Minshall et al. 1985).

While a lake may be considered to be a self-contained ecosystem, bioenergeticaly speaking (e.g. Forbes 1887; Thienemann 1953), it is, nevertheless, influenced by external forces. Allochthonous detritus, meteorological inputs such as wind-borne particulate matter, dissolved substances in precipitation, atmospheric gases, and geological inputs such as nutrients dissolved in groundwater, inflowing streams, or runoff are all important elements in lakes (Schindler and Nighswander 1970; Smith 1980). Moreover, nutrient and energy sources may be divided between allochthonous and autochthonous sources, depending on the successional stage. In consideration of a trophic cline of lakes from those low in nutrients (oligotrophie), to those high in nutrients (eutrophic), the latter must rely relatively heavily on allochthonous materials, while oligotrophic lakes may be able to recycle much of their own nutrients derived from autochthonous sources., As a rule, the allochthonous

TABLE 5. A comparison of some trophodynamic processes, especially as applied to north-temperate rivers and lakes.

Attribute	Rivers	Lakes
Primary energy and nutrient sources	Allochthonous	Autochthonous
Secondary energy and nutrient sources	Autochthonous, meteorological and geological inputs; tributaries and seepage	Allochthonous, meteorological and geological inputs
Allochthonous/autochthonous ratio	Decreases in downstream direction	Decreases with increasing age in eutrophic systems
Rate of nutrient influx	Governed by terrestrial vegetation, flooding	Determined by internal cycling rates
Speed of nutrient transit	Rapid; determined by gradient and current	Slow; determined by wind and waves, and overturn
Nutrient retention	Low	High
Course of nutrients	Downstream progression; constant renewal of dissolved nutrients; nutrient spiralling	Nutrients primarily recycled in place

Data were derived, in part, from the following sources: Hynes 1975; Webster 1975; Welcomme 1979; Moss 1980; Smith 1980; Minshall et al. 1985.

component of energy and nutrient input via leaf litter is relatively low in lakes. This is due, in part, to the low rate of inflow in lakes, and the reduced effect of the riparian zone in the offshore waters. However, the fact that autochthonous sources play a more important role in lakes (Table 5), is due to the relatively large water volumes at the lake's surface that are conducive to photosynthesis and hence, primary production. On the other hand, autochthonous sources in rivers generally supply a smaller amount of energy and nutrients due, in part, to high turbidity levels, a near absence of phytoplankton, and relatively few macrophytes, although the effect increases downstream (e.g. Vannote et al. 1980).

Hynes (1975) described riverine ecosystems as being largely heterotrophic, in the sense that they continually derive energy from upstream sources. However, strongly autotrophic regions often exist as well, especially in the midreaches, according to Vannote et al. (1980). Autotrophic components may, therefore, make considerable contributions to the primary production in a river (Hynes 1963; McIntire 1975), especially in large rivers and flood plain systems (Sedell et al. 1989). Therein, a general pattern emerges, which is applicable to many lotic communities: the headwaters, if shaded, are primarily heterotrophic; at the midreaches, where the effects of the riparian vegetation are reduced, autotrophy increases; and further downstream in more turbid waters the river reverts back to heterotrophy.

Secondary sources of biotic energy in rivers generally include subsurface seepage (Welcomme 1979), precipitation, and tributary inputs (Table 5). In some areas, where rocks are poor in nutrients, and the soils are leached (as in the case of tropical laterites), precipitation may indeed account for the primary input of stream nutrients (Welcomme 1979). Tributaries may enhance the levels of nutrients in the main stem if the concentrations of nutrients and/or food items in the tributaries exceed those of the main channel (Ryder 1964; Minshall et al. 1985). Alternatively, a tributary may serve to dilute nutrient concentrations or provide a new avenue for the influx of coarse particulate organic matter. Hence, the characteristics of a particular stream section, downstream from the influent of the tributary, may be reminiscent of the upstream reaches.

The rate of nutrient influx also depends largely upon the degree of flooding and the numerous effects of the terrestrial zone (Sanders 1972; Hynes 1975). Flooding results in the input of a large amount of fine particulate organic matter; also, the water entering the stream following flooding contains high levels of dissolved organic matter (Hynes 1975). Local flooding of banks may occur as well, due to the natural obstructions present in the water column, thus providing an additional source of nutrients (Sanders 1972).

The unidirectional flow, so characteristic of rivers, results in a rapid transport of nutrients in a downstream direction (Table 5), especially where nutrient retention mechanisms are limited. Both producers and consumers must be adept at rapid nutrient uptake, therefore, especially the sessile biota which cannot pursue their food items. The river biota essentially depend upon the steady nutrient replacement via allochthonous debris and nutrient or detritus displacement from upstream.

Nutrient retention mechanisms within rivers allow processing and nutrient distribution in localized stream sections. Thus impeded, food is rendered available to riverine biota (Speaker et al. 1984). High gradient streams, typified by steep slopes, often have a high leaf litter input as well as a high rate of retention (Sanders 1972). Important retentive features of rivers include debris dams (Triska 1984), macrophytes (Benfield 1981), and riparian zone vegetation (Cummins et al. 1984), in the form of roots and overhanging, partially submerged branches, as well as the large tree trunks from which they are derived. Logs or fallen trees are important retention mechanisms which sometimes cause flooding of the riparian zone, thus forming oxbow lakes, multiple channel rivers, and other complex habitats (Sedell and Froggatt 1984; Minshall et al. 1985). Subsequently, trees may drown and eventually represent a further addition of allochthonous material to the river.

Some nutrient cycling in place occurs in rivers where materials are retained by obstructions (such as those listed above); hence, the loss of some fine particulate organic matter to downstream reaches is prevented (Benfield 1981). Webster (1975) termed the cyclic downstream movement of nutrients in rivers "spiralling", and he noted that the process tends to maximize utilization of available fine particulate organic matter. The tightness and magnitude of the spirals is indicative of a stream's ability to process nutrients. Further, spiralling is a mechanism whereby stream ecosystems may withstand and recover from disturbances (Minshall et al. 1985). Invertebrate collectors may be instrumental in the retention process when they consume fine particulate matter (Wallace et al. 1977). In the highly retentive low orders (1–3), spirals tend to be tight, and conversely, they are separated by long distances in downstream locations (Minshall et al. 1985). Spiralling distance appears to be affected primarily by the current velocity and the frequency of retention devices, whereas biological processes are of less significance (Minshall et al. 1985).

Lentic ecosystems may be viewed as nutrient reservoirs, where internal nutrient cycling is an on-going process (Table 5). Unlike rivers, with their characteristic unidirectional, and rapid nutrient transport, demanding constant replacement from upstream, lakes are more self-sufficient in terms of nutrients. Lentic nutrients are recycled as a rule, and are subject to slow, current-induced movements through the water column or by migrations of the biota.

The rate of decay in rivers, or the microbial activity, depends upon the type of litter, ionic nitrogen availability, and probably the presence of phosphate or other chemicals (Hynes 1975). It would seem reasonable to assume that the decomposition rate is further influenced by the abundance and types of invertebrate consumers present in a certain stretch of river. Indeed, the reduction of lotic insect fauna may decrease shredding and other breakdown activity, subsequent utilization, and downstream transport of organic matter (Wallace et al. 1977). Warm temperatures may enhance the rate of decay by increasing microbial activity; hence the warmwater, high order streams may exhibit more rapid rates of decay. In light of the above, Wallace et al. (1977) consider the consumers to be the governing forces in both the transfer of energy and the recycling of nutrients.

Ecological Phenomena

Abiotic Controls

The contribution to stream environment by several morphological properties such as gradient, width, depth, substrate type, riparian vegetation, and other related factors, is enormous, and confounded by a myriad of interdependencies that vary from one stream to another (e.g. Minckley 1963; Hocutt and Stauffer 1975; Winger 1981). This pervasive morphological influence is complicated by the hydrodynamic properties of the stream. Accordingly, morphology, hydrodynamics and temperature are inextricably interrelated, and together they form the principal components of the abiotic milieu. These three abiotic parameters, to varying degrees, determine species distributions and abundance. Ergo, a stream gradient approaching the vertical may preclude the existence of virtually all inhabitants, except for those torrentially-adapted forms such as the hillstream loaches (Homalopteridae; Nelson 1976). In this example, gradient per se, appears to be a dominant, overriding force in influencing biota, and does so primarily through the agency of stream velocity.

Chemical effects on the stream environment, in general, are not paramount, unless one or more chemicals are so astoichiometrically imbalanced (Stumm and Morgan 1970) as to affect metabolism or growth of invertebrates or fishes. This happens but rarely in north-temperate streams, except for the often severe effects ascribed to anthropogenic inputs. For biotic considerations, chemical assessments of streams may, in effect, be nutrient assessments, particularly in the case of phosphorus. Chemical composition of stream water, therefore, may be more important as a determinant of their productivity rather than as a limitation to biotic distribution.

Lakes are also provided with an ambience suitable for their biota through their principal morphological properties, which together with climate, determine the seasonal hydrodynamics regime (e.g. Rawson 1952, 1960). Lake depth, area, and volume are closely correlated (Hayes 1957; Kerekes 1976), and in north-temperate dimictic lakes, are critical to the duration and extent of spring and fall overturns as well as wave dynamics, the two predominant features of hydraulic activity in lakes. These influence the chemical composition of lake water which is critical to their productivity, particularly the phosphorus content. As most of the primary productivity in lakes is dependent upon photosynthesis rather than on inputs of allochthonous detritus, nutrient composition of lakes becomes an important consideration, not only from a production standpoint, but also for the determination of species composition (e.g. Marshall and Ryan 1987).

Biotic Accommodation

Huet (1959) has categorized the running waters of Western Europe according to stream gradient or slope, and the cross-section of a stream and its valley. In his classification scheme, he identified characteristic properties for each of four "fish zones": the trout zone, the grayling zone, the barbel zone, and the bream zone.

Huet's (1959) stream classification noted changes in each zone, usually constituting a cline from headwaters to mouth. Hence, gradient, current velocity and dissolved oxygen generally decreased; while stream width and depth, discharge, temperature and turbidity increased, each factor having some influence in determining the species composition and abundance in any particular zone. While stream classification by zone or reach may be of little ecological value because streams are best viewed as gradients or continua (Cushing et al. 1983), we believe that there is significant practical merit to the former approach viewed from within the latter context. Accordingly, we propose that a zonal, or reach approach may be logistically valuable from a sampling perspective, to address a complex problem in a pragmatic and tractable manner. In this regard we concur with the conclusions of Macan (1961) in Hawkes (1975), who observed that any classification framework for stream ecology should be used — "to stimulate thought and further research, rather than [as] a cage to confine it." Zonal research should be planned, however, within the conceptual understanding of the River Continuum Concept (Vannote et al. 1980), and subsequent analyses effeeted accordingly.

Other stream classification systems have been proposed, some of greater complexity than Huet's (1959) relatively simple schema (e.g. Margalef 1960; Platts 1979). Most of these classifications are of considerable heurisitic value in any progression towards an increased understanding of stream ecosystems.

In lentic waters, vertical density zonation effectively stratifies temperature, oxygen, phosphorus and other nutrients and chemicals. The different zones of the water column are inhabited by different fish assemblages, particularly in oligotrophic lakes. For example, the warm upper, epilimnetic zone in summer, is typically inhabited by components of a percid community, while the lower, cold hypolimnetic zone contains salmonid community members. Hence, separation of two different fish assemblages living sympatrically within a dimictic lake, depends on depth and temperature primarily, while gradient and temperature would seem to be more important in streams. Segregation of fish assemblages in different lakes is dependent primarily on a lake's trophic level, particularly when measured in terms of temperature and phosphorus (Ryder and Kerr 1988; Ryan and Marshall in prep.).

Production, Diversity and Drift

Protoplasm elaboration by stream communities depends upon the various energetic inputs along the length of the river. Within stream orders, productivity varies according to substrate type such as bedrock and sand, which are the least productive (Smith 1980). A gravel-rubble bottom tends to be the most conducive to high levels of production, as it not only serves as shelter for invertebrates, but also provides a larger, more stable surface for the attachment of aufwuchs communities, and is eminently suited as a clean and well-oxygenated spawning substrate for fishes.

As a stream is traversed from headwaters to mouth, many factors combine to augment production rates, including higher water temperatures, increased photosynthesis, greater drift volume, higher nutrient levels, greater area of incident solar radiation, more fine particulate organic matter, as well as other factors (e.g. Hynes 1970; Vannote et al. 1980; Minshall et al. 1985). Factors detrimental to production going downstream may include increased inorganic turbidity and decreased oxygen levels. Production/biomass ratio is lowest at the headwaters, gradually increasing downstream, with greatest production levels occurring at the mouth.

In lakes, the highest production levels occur in eutrophic waters, and lowest in oligotrophic waters (Hutchinson 1957; Wetzel 1975). Primary production in lakes is mainly dependent on photosynthesis by pelagic algae, periphyton and littoral macrophytes. Essential to the production processes in lakes is the biofeedback of autochthonous nutrients, in contrast to the normally unidirectional flow of nutrients in rivers. Rivers, therefore, tend to be more open-ended than lakes, and depart further from the definition of a microcosmic system sometimes applied to lakes (e.g. Forbes 1887).

Taxa diversity in running waters is both a spatially variable attribute (generally highest in the middle orders; Vannote et al. 1980), and a temporal variable for any given reach. Hence, certain taxa are sequentially replaced by other taxa at any given stream location, dependent on the mean levels of specific environmental variables. This temporal diversity is seasonally determined, and as one taxon is drawn further and further from its seasonal optimum, another functionally similar species is drawn closer, and physically and functionally replaces the first organism (Cummins 1974; Minshall et al. 1985).

Biotic diversity in lakes tends to be more stable over time, and is more likely to be exemplifed temporally, in terms of cohort diversity, rather than species succession. Greatest species diversity in the north-temperate zone occurs in mesotrophic lakes where species may be drawn from as many as three community types (Ryder and Kerr 1978).

Organic drift (Waters 1969; Müller 1974), comprised mostly of particulate matter and invertebrates, is a stream phenomenon not known in lakes. It presents a more or less continuous stream of food organisms to both fishes and invertebrates without the necessity for energetic losses experienced by lake fauna in search of their prey. This passive mode of feeding in rivers, however, necessitates the maintenance of position in the water column. In certain instances, fishes feeding on drift may assume levels similar to fishes feeding *ad libitum* in aquaria, which likely explains why running waters are typically much more productive than their standing-water counterparts at the same latitude (Odum 1956; Blum 1972).

Reset Events

Periodic, natural events in lotic environments, such as seasonal floods or drought, may be traumatic to indigenous stream biota. These externally induced traumata may also be episodic in frequency and essentially unpredictable in terms of their temporal sequencing. Both types of destabilizing events, whether of periodic or episodic occurrence, are termed reset mechanisms, or simply, resets (Cummins et al. 1984; Minshall et al. 1985). Resets are generally associated with the lotic environment, but are not exclusive to them. Because streams are much more vulnerable to exogenous effects than are lakes in general, stream resets tend to be more dramatic, even temporarily traumatic, to stream communities. Nonetheless, the trauma is usually short-lived, and resets are now believed to be essential to the maintenance of normal community structure in streams (Cummins 1977; Cummins and Spengler 1978) through the relegation back to pioneer community status (Cummins et al. 1984). Stream organisms are well adapted to both regular and irregular resets, and recuperate quickly through the use of one or more adaptive mechanisms (Minshall et al. 1985).

Stream resets are often introduced through flooding and subsequent scouring of the stream bed and banks. In unprotected substrates the mean age of some invertebrate populations remains relatively young due to repetition of this process, while in protected environments, invertebrate populations are skewed towards old individuals (Minshall et al. 1985). In the north-temperate climatic zone, floods during the spring spate may be particularly damaging, not only to the stream bed and banks, but also to the riparian vegetation and stream fauna. This effect is induced following a buildup of an ice dam which may raise the water level markedly. The combined effects of warming weather and water accumulation eventually cause the ice-dam to break, and a massive volume of water and ice flush suddenly downstream, both in the main channel and along the flood plain on either side of the main stem. This phenomenon on large rivers has reached extreme levels known to uproot trees and wipe out human dwellings.

Reset events on lakes are generally less damaging to the environment and, therefore, less traumatic to the biotic communities. Spring and fall overturn may be considered "low key" reset events of only minor significance in terms of community alteration, although ecologically important for other reasons. Their main effects are to redistribute the community components according to their preferred temperatures, and to recycle nutrients.

Autumnal, equinoctial storms, accompanied by high winds and rain, may constitute a more severe and damaging reset event on large lakes. Damage would be greatest at the nearshore littoral zone, and fauna and flora there would be most affected. On the other hand, some species such as lake trout, seem well adapted to such incidents. Successful reproduction of lake trout, in general, obliges them to spawn on clean, windswept shoals in the fall (Martin 1957), and periodic, equinoctial storms may be instrumental in providing these ideal conditions.

Hyporheic Zone

The hyporheic zone (Orghidan 1959), that subterranean portion of a river that lies between the surficial substrate deposits of the rhithron and the phreatic (groundwater) zone, has been an enigmatic and much neglected stream biotope (Hynes 1970; Pennak and Ward 1986). It has often been observed that rivers are in ''intimate contact'' with groundwater aquifers (Ward and Stanford 1988) and that their interactive nature exerts a strong influence on habitat conditions. The hyporheic zone has been recorded as deep as 4.2 m under the substrate of the main river channel (Stanford and Gaufin 1974). In Europe, it has been observed to extend laterally under river banks for at least 3 m (Orghidan 1959), and in North America it may exceed this, extending as much as 50 m (Stanford and Gaufin 1974).

Within our present context, the hyporheic zone may be viewed as a unique refugium of streams, that mitigates or biologically buffers the traumata induced by reset events, and provides a constant faunal reservoir for post-reset conditions. There, shelter is provided for many invertebrate organisms (e.g. Pugsley and Hynes 1986), which may permit them to escape physiological stress from extremes of temperature and current, droughts and floods, or predation (Orghidan 1959; Hynes 1970).

Within the substrata of most lakes, conditions required for the establishment of an inhabitable hyporheic zone of any substantial depth do not exist. Eutrophic lakes in particular, have deep layers of organic sediments overlying their substrates, which may create inhospitable living conditions for aerobic organisms, due to the by-products of putrefaction (e.g. Hutchinson 1957; Mortimer 1971). In these instances, only a few centimetres of substrate immediately below the mud–water interface zone may be inhabitable by facultative anaerobes. Studies in Swedish Lake Malaren, a mesotrophic lake with dissolved oxygen in the bottom waters generally in abundant supply, showed invertebrate organisms no deeper than 20 cm within the bottom muds (Milbrink 1969). Only the wind-swept and wave-washed littoral of oligotraphic lakes offer anything akin to a stream environment for benthic organisms (Borner 1917 in Brinkhurst 1974; Kitchell et al. 1977). There, the large particle size of the substrate materials and the continual removal of fine organic sediments through wave action, allow for deeper penetration of the bottom by aerobic organisms. Nonetheless, a true hyporheic zone in the sense of Orghidan (1959) is only approached but not attained in lakes. As most reset events for lakes are not as traumatic as those for streams, a deep substrate recolonization refugium for lakes would not likely be an ecological necessity.

Community Dynamics

The ways in which aquatic communities achieve dynamic equilibrium differs between streams and lakes. Fish assemblages for example, are said to be stochastic in streams, because of periodic extinctions of species due to reset events, followed by recolonization from riverine refugia (Grossman et al. 1982). This stochastic school of thought holds that dynamic equilibrium is not possible in stream fish assemblages as it is in lake fish communities which are deterministic systems, because the physico-chemical environment is rarely stable enough for the achievement of steady-state. It follows, therefore, that stream assemblages of fishes are highly variable in their composition and therefore, unpredictable. In general, the well-being of stream fishes is determined more by environmental variability than by biotic interactions.

Recently, it has been proposed that stream assemblages have aspects of both stochasticity and determinism, the latter resulting in a higher level of predictability (Minshall et al. 1985; Schlosser 1985). The deterministic aspects of lotic ecosystems are exemplified by the apparent resiliency of stream biota to reset events.

With respect to lakes, communities tend to be even more deterministic and therefore, more predictable. This is all relative, of course, and applies principally to integrated, coevolved assemblages of species, sometimes called harmonic communities (Ryder and Kerr 1978). Harmonic communities in lakes are subject to organizational distortion both seasonally and from year to year, but unless subjected to a cataclysmic event, tend to retain their fundamental identity. Astatic assemblages of fishes or other organisms (e.g. Ryder and Kerr 1978) are usually formed through human intervention, and have a tendency towards greater stochasticity and less predictability.

Vegetation Controls

Stream flora are comprised for the most part of periphyton and macrophytes, phytoplankton being relatively unimportant except for the slowest flowing reaches (Table 6). The ratio of autotrophy to heterotrophy generally increases from insignificant levels in the heavily shaded, low order streams to a maximum in the wide, intermediate stretches. The microproducers (e.g. diatoms, blue-green algae, green algae, water mosses) and macroproducers, or vascular plants, are the primary photosynthesizers in the middle reaches (Cummins 1974; Sumner and Fisher 1979). The intermediate stream sections, as well as the high orders, are noted for the presence of phytoplankton, especially in large rivers (Cushing 1966), except for those areas where velocity, turbidity, temperature, and nutrients may be limiting (Hynes 1970; Benfield 1981). While primary productivity in some stream reaches may be limited by the amount of shading by the riparian forest, as well as the water's chemical composition, the shading of lentic waters is relatively less extensive, as are turbidity levels, thus allowing enhanced pelagic algal growth. In lakes, where water levels are more stable, phytoplankton tends to be discontinuously distributed, but essentially ubiquitous in the euphotic zone (e.g. Hutchinson 1961).

Certain features are compensatory, however, for the generally lower light regime in rivers. The transport and removal action of the current greatly enhances processes such as photosynthesis; thus, lotic primary production is somewhere on the order of 6–30 times higher than observed for primary production in lentic environments (Table 6; Odum 1956; Nelson and Scott 1962; Hynes 1963; Blum

1972). Production is heightened as the current disseminates reproductive bodies and rids local areas of excretions and excreta, while cleaning and releasing the more firmly attached species (Blum 1972; Benfield 1981). Moreover, lotic species may exhibit higher respiratory rates and more efficient mineral uptake than the related lacustrine species (Whitford and Schumacher 1961). Other adaptations by stream vegetation, aside from macrophytes (Hynes 1970), enhance nutrient uptake; for example, a large surface-to-volume ratio and a body form which allows maximum contact with the moving water, have evolved in a lotic environment (Blum 1972).

Upstream plants are able to maintain a competitive advantage over downstream plants, the former being in a more logistically favorable position from which to garner the dissolved nutrients, which are constantly renewed through runoff or ground water (Blum 1972). In some systems, however, it would seem likely that these effects of relative stream position may be compensated for, or overidden by, the rate of nutrient influx via runoff, subsurface seepage and tributaries. The sporadic, unpredictable nutrient influxes may be responsible for the low "equability" (or eveness of distribution of some specimens among species) in rivers as noted by Patrick (1972).

Primitive Plants

Of the primary producers in rivers, algae are most important (Table 6; Patrick 1972). Some species are believed to have evolved within rivers (Hynes 1970); in fact, they appear to possess an "innate current demand", according to Benfield (1981). The many adaptations of lotic algae, including opportunistic growth (Benfield 1981), presumably allow their rapid recovery from setbacks such as reset mechanisms, or other periodic or episodic events discussed earlier. Hynes (1970) noted that the "epipelic" (mud-dwelling) habits of some species enable them to retain their position within the stream. Others are "epilithic" (living on stones or similar objects) and thus, they anchor themselves via a stalk or a jelly-like substance. He also mentions that the thallus, another feature promoting algal stability, may be flattened so that a larger surface area is adherent to the substrate. Yet other species of algae are endowed with a cushion-like shape, which diverts water flow over them; or rhizoid-like structures at the bases of filaments, sometimes exceeding 1 m in length, to aid in anchoring algae to the substrate. Finally, higher respiratory rates are also important in lotic algal survival (Whitford and Schumacher 1961).

Aquatic Macrophytes

Hynes (1970) observed that rooted plants have no notable morphological adaptations to running water, aside from their tough, flexible stems and their creeping-growth habit (stolons, rhizomes, adventitious roots), which allow them to maintain their position on the stream bed (Table 6). He noted that current-induced reductions in size, however, are commonly observed in rooted plants. The same plant species may vary markedly in appearance, depending on whether it is found in a lotic or a lentic environment, or whether it is exposed to or sheltered from the current. For example, the upstream and laterally-directed leaves found within a single clump of *Nuphar luteum* plants may be more reduced than those which they protect from the current (Hynes 1970). Furthermore, certain plant types tend to be successful on particular substrate types. The lack of riverine adaptations may be a reflection of the recent glaciation in the north-temperate zone, which suggests that macrophytes may have been derived from lake habitat. Hynes (1970) found that the following are controlling factors in the success of rooted plants: (1) current speed; (2) water hardness; (3) the frequency of strong, sudden outbursts of water (i.e. flooding); (4) light; and (5) nutrients. In view of this, macrophytes contribute progressively more to the primary production in areas of low gradient and shallow water (Benfield 1981), and in regions where the above factors are not limiting.

Floating plants are relatively rare in north-temperate lotic environments; however, they assume a much greater impor-

TABLE 6. A comparison of selected adaptive attributes of stream and lake flora, especially as applied to the north-temperate zone.

Attribute	Rivers	Lakes
Effects of riparian vegetation shading	Extensive	Insignificant
Major contributors to primary production	Microproducer, macroproducer and periphyton; phytoplankton in large rivers	Phytoplankton and macroproducers;
Production-to-biomass ratio	Increases downstream	Increases near shore
Primary productivity	Relatively high	Relatively low
Respiratory rates	High	Low
Mineral uptake rates	Rapid	Slow
Floral distribution	Reliant upon nutrients, current	Dependent on depth, substrate
Phytoplankton abundance	Low; greatest in intermediate or high orders; limited by turbidity, turbulence	High
Algal adaptations	Numerous, attached	Primarily pelagic
Bryophytes/lichens	Prevalent; fast-flowing areas; shade tolerant; some limited by hard water	Scarce
Macrophyte adaptations	Few restricted to running waters	Many
Floating plants	Limited to slow-flowing reaches; prevalent in tropical rivers	Restricted to sheltered bays

Data were derived, in part, from the following sources: Odum 1956; Nelson and Scott 1962; Whitford and Schumacher 1964; Cushing 1966; Hynes 1970; Blum 1972; Patrick 1972; Cummins 1974; Welcomme 1979; Benfield 1981; Cummins et al. 1984.

tance in the tropics (Hynes 1970) where high levels of turbidity give them a competitive advantage over submerged plant species.

Lentic ecosystems differ from rivers in that they are characterized by more stable water levels, a factor favorable to aquatic macrophytes (Table 6). The water stability also eliminates the need for algal anchoring to the substrate; consequently, lentic algae are predominantly pelagic. In the euphotic sector of the pelagic zone, algae can also capitalize on high levels of solar radiation. Standing waters, then, are more conducive to both phytoplankton (Welcomme 1979) and macrophyte growth. Mosses, while generally rare in lakes, are sometimes present where the euphotic zone intercepts the littoral zone.

Faunal Adaptations

Zooplankton

Faunal assemblages of certain stream sections have long been linked to the prevailing physical conditions (e.g. Adams 1901; Hynes 1970). Zooplankton growth, for example, is generally very slow in the main stem of a flood plain river (Table 7) due to the swiftness of flow, high turbidity levels, and low dissolved oxygen (Hynes 1970; Welcomme 1979). Nevertheless, the generally turbid, high order river is likely to contain more zooplankton than the low order reaches, due to the more lentic characteristics of the former, the periodic influxes of drift and plankton along the length of the river, and the resultant nutrient enhancement downstream.

Lakes tend to harbour a pelagic zooplankton community of relatively high stability and abundance. Here, the limiting factors common to the lotic environments (e.g. unidirectional flow, high turbidity) are not sufficiently great to represent the same severe growth restraints.

TABLE 7. A comparison of selected adaptive attributes of stream and lake fauna, especially as applied to the north-temperate zone.

Attribute	Rivers	Lakes
Zooplankton growth	Low; greatest in high or intermediate order streams; limited by turbidity	Considerable; limiting factors less significant
Boundary layer	Present; shelters benthic organisms	Absent
Invertebrate predominance	Headwaters	Littoral
Primary fish forage	Invertebrates	Forage fishes
Typical morphological characteristics of fishes	Stream-lined; round to oval in cross-section	Deep-bodied; laterally compressed
Adaptations of fishes	Numerous; adaptive to a turbulent, turbid environment	Numerous; adaptive to pelagic and bathypelagic conditons
Climatic stresses	Severe; extreme temperature fluctuations in summer; ice formations and near-freezing temperatures in winter	Moderate; limited by low levels of dissolved oxygen in winter
Production/ biomass ratio	Increases downstream; maximum in 3rd to 5th order streams	Increases near shore

Data were derived, in part, from the following sources: Varley 1967; Hynes 1970; Welcomme 1979; Moss 1980; Moyle and Cech 1982; Ward 1985.

Invertebrates

Lotic invertebrates exhibit many types of adaptations to swift water. Some protection from the current is afforded them within the "boundary layer" (Table 7; Ambühl 1961), a layer of water a few millimetres in thickness, just above the substrate, where the current speed is considerably lessened and smooth flow results (Hynes 1970; Moss 1980). A flattened body has evolved in some species, as in the dorsally compressed mayflies (e.g. *Baetis* spp.), which allows them to lie flat and protected within the boundary layer, or crawl under stones for protection (Varley 1967; Moss 1980). Moss (1980) noted that some organisms use suckers to cling to rocks (e.g. snails and dipterans), while certain adaptive features, including small movable spines, hooks, grapples, and claw-like legs, allow various other species to maintain a foothold. Silk pads, functioning either as a receptacle for hooks or as an asylum for cocoons, are also spun by various species (Moss 1980). The longitudinal succession of species associations, as described for fishes (Huet 1959), is also in evidence for invertebrates (e.g. Varley 1967; Ward 1986).

While some invertebrates are unique to lotic ecosystems, numerous specializations for a limnetic existence occur as well (e.g. Hynes 1970; Pennak 1978). The absence of both continual, unidirectional turbulent flow, and a boundary layer in lakes, remain two of the most conspicuous differences between the two systems; hence, the lentic benthos component does not require numerous turbulence-related adaptations. While the water velocity appears to have a major influence on the abundance of riverine invertebrates, the production of bottom fauna in large deep lakes may be largely determined by morphometric conditions (Rawson 1953), substrate type, and dissolved oxygen levels.

Invertebrates are numerous in the headwaters of rivers, and as a result, predation is widespread there. Hynes (1970) discussed the great significance of invertebrates in the diets of most riverine fishes. Terrestrial insects are not as important in the diet of lake fishes; rather, forage fishes are consumed extensively by many lentic piscivores, while crustaceans and aquatic insects constitute another sizable prey component.

Fishes

An astounding variety of adaptations has developed for fishes in fluvial environments; presumably, this is due to the long-standing history of fishes' occurrence and evolution in rivers, especially in Europe (Balon et al. 1977). Fishes characteristic of turbulent waters are generally streamlined, and round (or oval) in cross-section according to Varley (1967). In combination with the predominant red muscle (adaptive for sustained swimming power) of river fishes, such a shape facilitates movement upstream, enabling fishes to maintain their positions against the current. Other species may possess adhesive disks, or a dorso-ventrally flattened shape, with which they can counter the effects of current (Varley 1967). Alternatively, swimbladders may be absent in some stream fishes (Scott and Crossman 1973; Kuehne and Barbour 1983), as effective buoyancy regulation is not necessarily crucial to riverine fish existence.

Adaptations also exist among river fishes which facilitate movement in a nocturnal or turbid environment (Table 7; Ryder 1977). Frequently, these fishes possess a tapetum lucidum (e.g. Moore 1944), electrical organs (Lissman 1963), barbels or an advanced acoustico-lateralis system (Alexander 1967). The eyes of river fishes may be dorsally oriented for optimum light gathering, or reduced as a protection against suspended particles.

Other riverine fish adaptations may range from air-breathing in slow-flowing flood plain rivers (Cummins 1972) to the subterminal, protuberant mouth of some river fishes, which is a convenient mechanism for scouring the bottom for food.

Welcomme (1979, 1985) identified two types of behaviourally distinct flood plain fishes. The first group, termed "whitefish", migrate to the main river channel when severe conditions in the flood plain render it necessary. "Blackfish", on the other hand, are extremely tolerant of deoxygenated conditions (Welcomme 1979). Analogous to the African "whitefish" phenomenon in North America, are the movements of fishes into the mouths of tributaries to avoid certain stress conditions, such as low dissolved oxygen (Gammon and Reidy 1981) or low temperatures (e.g. Sprules 1952; Brett and Alderdice 1958).

Flood plain fishes may possess unusual and highly specialized adaptations. For example, Welcomme (1979) reported "upside-down" swimming positions (allowing effective browsing on submerged nearshore roots), burrowing in sandy substrates, serpentine shapes, and the small size of certain species. The two latter features facilitate movement through entangled vegetation, and enable fishes to hide within the vegetation.

The fishes of lentic, or slow-moving waters, may differ considerably in structure from those of rivers. Lake fishes are typically deep-bodied and laterally flattened, or disk-shaped (Varley 1967). In accordance with a frequent pelagic existence, these fishes are often silvery, with relatively large, laterally oriented eyes. White muscle is the primary muscle type possessed by lake fishes; hence, many lentic species might not tolerate life in swift rivers, as they would not have the sustained energy resources necessary to withstand the current for long periods (Varley 1967). Swimbladders are almost essential as buoyancy regulators in lentic waters, which are of a relatively great mean depth (except for certain demersal species such as *Myoxocephalus quadricornus*). In addition, the neuromast canals, so extensive and functional in a riverine stone loach (Cobitidae), are absent altogether in another loach that is an inhabitant of still water (Alexander 1967).

The lotic fish fauna must be adept at survival in a dynamic, seasonally variable habitat. In summer, the drastic hourly and diurnal temperature fluctuations probably represent a thermal stress to stream fishes (Brown 1969; Hynes 1970). Austere and rigorous winter conditions may pose an even greater threat to fish survival, resulting occasionally in high mortality rates (Maciolek and Needham 1951; Reimers 1963). For example, extreme water level and temperature fluctuations are quite common during winter, and the combined effects tend to stress trout. Therefore, poor, post-winter body condition may often be attributed to excessive, temperature-induced catabolism (Reimers 1963). Hunt (1969) suggested that the warmer temperatures of Lawrence Creek, Wisconsin, were partially responsible for an enhanced overwinter survival rate there.

Despite its often adverse effects, winter represents a mixed blessing to stream biota. Maciolek and Needham (1951) noted, for example, that snow and ice may shield biota from both the cold and predators. Frazil ice seemed to alter stream morphology periodically, but there was no obvious sign of harm to the fishes on a short-term basis. In their study of Convict Creek, California, Maciolek and Needham (1951) revealed that while rapid increases in flow (sometimes doubling between early morning and noon) displaced many aquatic organisms, this proved to be of benefit to trout, which could feed more readily on riffle-dwelling insects.

Overwintering lake fish species are subjected to climatic stresses which vary somewhat from those in rivers. Ice may be a limiting factor in fish survival; however, this is largely in the sense that it prevents wind-activated aeration of the water, a major source of oxygen during ice-free seasons (Wetzel 1975). When dissolved oxygen levels are insufficient for respiration, a considerable "winterkill" of fishes may ensue (Greenbank 1945). In general, winter conditions in lakes (with the exception of dissolved oxygen insufficiency) are more benign than those in rivers and, therefore, less stressful to lentic biota.

Studies concerning lotic fish yields, particularly in north-temperate rivers, have been sorely neglected in the past. Yield measurement in warmwater streams, as elsewhere, has been plagued with difficulties, due to the mobility of both fish and fishermen in such lengthy, open-ended systems (Larimore 1981). In pioneering studies, however, Welcomme (e.g. 1976, 1979, 1985, 1989) correlated yields with water conductivity, river length, drainage basin area, and maximum flooded area in tropical flood plain rivers. Platts et al. (1983) suggested that a measure of stream width or mean depth would allow an estimate of fish standing stocks and biomass per unit area. Platts (1979) also suggested that the magnitude and frequency of orders in Idaho streams would provide general information on fish species present, as well as estimates of standing stocks within single planning units; however, this view is not shared by all workers (e.g. Hughes and Omernik 1981). In general, all work pertaining to definitive, quantitative measures of fish yields in lotic systems has, until recently, been directed towards moderately small streams.

Studies involving estimates of standing stocks, production and yield of lakes are legion and have been extensively documented (e.g. Ricker 1975; Bagenal 1978). Predictive models are sufficiently sound to be able to estimate total fish yields from large lakes and reservoirs with a satisfactory degree of precision for management purposes (e.g. Ryder 1978b).

Final Integration and Evaluation

Our stated intention within this paper is to examine the world's rivers within a lake ecology context (Thienemann 1953); to identify areas of commonality and contrast between rivers and lakes (Table 8), where concepts and methodologies may be transferable from a comprehensive lake data base to a deficient one for streams; and finally, to explore unifying concepts in ecology (van Dobben and Lowe-McConnell 1975) that will allow comparable approaches to the fisheries management of both lake and river ecosystems (Regier and Henderson 1980). Accordingly, our level of comparison has been both restrictive and selective, rather than exhaustive, and we have sought to garner, synthesize, and comprehend the various insights included in the recent literature in preference to proferring new analyses of our own.

Our initial impression upon surveying a substantial part of the stream ecological literature of the recent past, has been the relatively large contribution made towards the understanding of these complex ecosystems by Vannote et al. (1980) through their River Continuum Concept. Their concepts have synthesized, clarified and generalized much of what was known about stream ecology until recently; a more topical contribution to the literature by Minshall et al. (1985) has crystallized the concept even further. The River Continuum Concept likely represents a new paradigm in the field of stream ecology (in the sense of Kuhn 1962). As such, it is a convenient launching pad for future endeavours that attempt to describe and quantify the aquatic biota of its streams and rivers, with a particular but practical bent towards the assessment of potential fish yields. The new synthesis of stream ecology provided by the River Continuum Concept and complemented by the comparative approach herein (river ecology vs lake ecology), would seem to provide a rapid entry into a complex and often controversial subject (e.g. Statzner and Higler 1985). Our further focus on stream ecology from a broad lake perspective will hopefully provide a common basis that will permit science transfer where appropriate, as recommended by Ricker (1934).

TABLE 8. Some qualitative differences between rivers and lakes.

Differences	Rivers	Lakes
Major energy source	Detritus	Solar radiation
Nutrient regime	Spiralling	Cycling
Reset events	Floods (severe); ice scouring	Overturn (moderate)
Fragility	Fragile; rapid recovery	Well buffered; slow recovery
Resilience	High	Low
Community structure	Sequential (seasonal); successional (spatial); mainly stochastic	Harmonic; successional (temporal) mainly deterministic
Community refugium	Boundary layer; hyporheic zone (i.e., deep, inhabitable substrate)	Ecotone; shallow, inhabitable substrate

Data were derived, in part, from the following sources: Hynes 1970; Cummins 1974; Webster 1975; Ryder and Kerr 1978; Vannote et al. 1980; Grossman et al. 1982; Holling 1985; Minshall et al. 1985.

Our previous observations outlined similarities and differences between lakes and streams in a somewhat detailed, but non-exhaustive fashion. Now we wish to draw attention to certain commonalities of rivers and lakes through a more generalized "compare-and-contrast" exercise. On that basis, we will compare rivers and lakes from the perspective of a series of several pairs of dichotomies (Fig. 1A-F). Each dichotomous pair is clinal in nature, and represents a gradient or continuum between two polar extremes. The gradient in each case is unlikely to be perfectly linear, although in certain instances linearity may be approached.

Each of our comparisons will be done from within a *caeteris paribus* context and a somewhat arbitrary or subjective point of view. Our casually derived constructs are intended to focus attention on important distinctions between lotic and lentic environments, and thereby provide an heuristic understanding of the similarities and differences of the two subsystems. Other observers may, with equal justification, make different distinctions.

Accordingly, our observation that rivers are horizontally oriented while lakes have a vertical orientation, does not preclude the converse condition, nor does it fail to recognize that both orientations exist in each instance, but rather places emphasis on an important ecological principle, that within an ecosystem, lakes provide a storage function (vertical orientation), while rivers which form connecting links within a complex matrix, are primarily vehicles for communication and transport (horizontal orientation).

Space-Time Organization

Most physical, chemical and biological phenomena in rivers are spatially organized (Fig. 1A), that is, marked differences occur as the stream is traversed from headwaters to mouth. This spatial organization applies to ecological succession, nutrient inputs, production processes, stream velocity, dissolved solids concentrations, and the structure and function of lotic communities (e.g. Vannote et al. 1980). Many other natural phenomena in rivers are also structured horizontally in a clinal fashion, from headwaters to mouth.

Implicitly, a disturbance or human intervention at any point on a river system, such as a massive spill of contaminants, might be expected to have dire consequences on the stream reaches below the input, but have next to no effect upstream. While this spatial dependency augers ill for stream fragility, it might be equally considered as beneficial to stream rehabilitation prognoses, especially its inherent high level of resiliency (Table 8). Accordingly, a massive episodic spill of contaminants into a river system might be expected to be rapidly flushed downstream and quickly replaced with water form the uncontaminated upper reaches, except for those toxic substances that may be trapped in organic bottom sediments or absorbed by the biota. Even there, floods during the spring spate, accompanied by ice-scouring, may cause toxic-laden sediments to be rapidly flushed out, at least on an annual basis.

Lakes, on the other hand, appear to be more temporally organized. Flushing rates (water renewal times) for lakes may vary from a few days to hundreds of years, depending

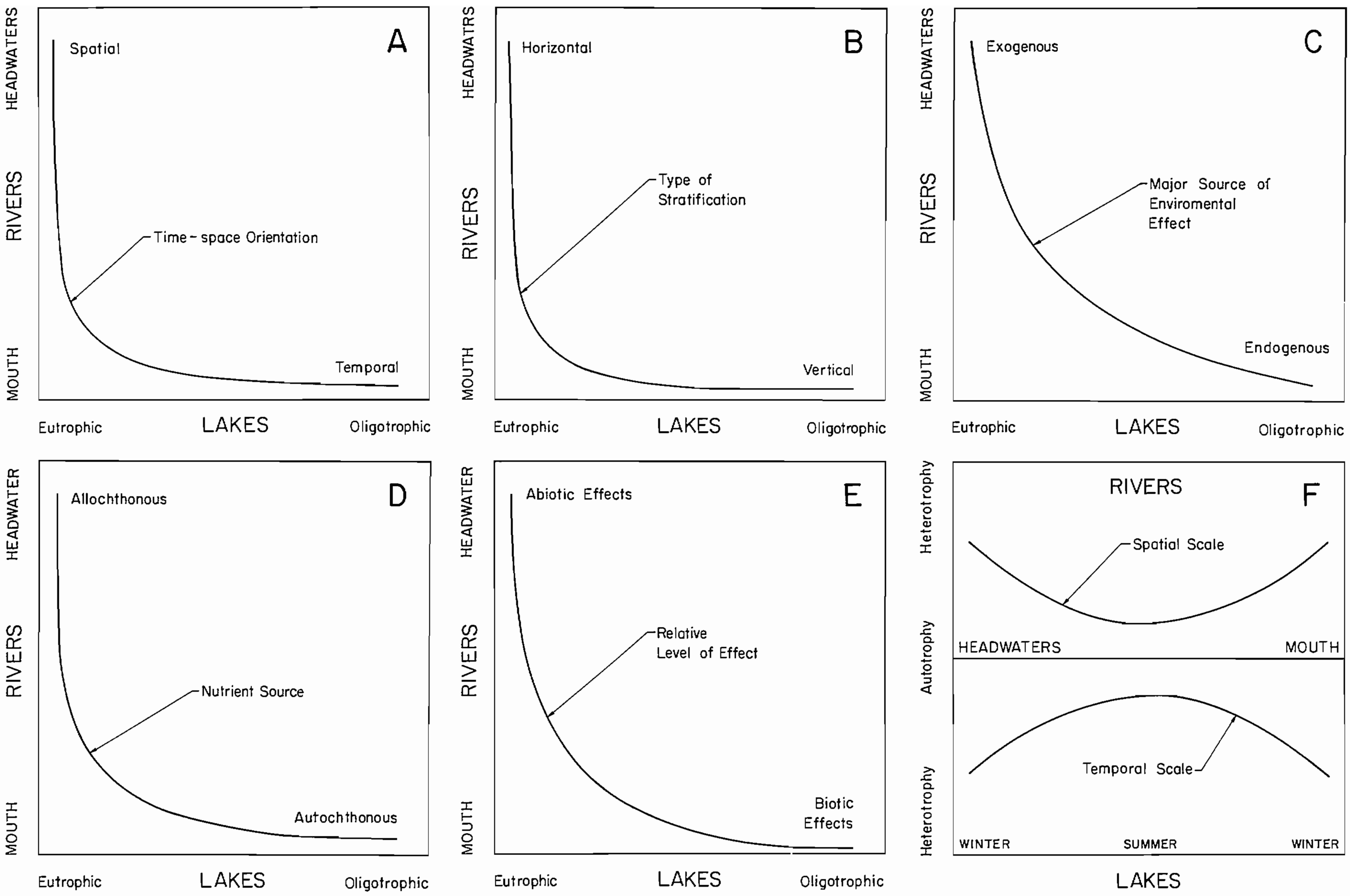

FIG. 1. Six dichotomous pairs of ecological properties which emphasize the polarization of rivers and lakes: A — many ecological properties of rivers tend to vary spatially from headwaters to mouth, while comparable properties of lakes vary temporally over time (i.e. ecological succession); B — oxygen and nutrients (as examples) are horizontally stratified in rivers but vertically stratified in lakes; C — environmental effects are mostly exogenous in rivers and endogenous in lakes; lakes, therefore, have more efficient feedbacks which tend to retain them at dynamic equilibrium; D — rivers receive higher percentages of allochthonous nutrients than lakes, the latter depending to a greater extent on internally recycled, or autochthonous, nutrients; E — abiotic effects tend to have the greatest influence in lotic environments while biotic effects are proportionately greater in lakes; F — in rivers, the ratio of heterotrophic production to autotrophic production, which is spatially oriented, is high at the headwaters and mouth, and low in the middle reaches; a similar ratio for lakes varies temporally, being highest in winter and lowest in summer when primary production is high.

on their volume and rates of inflow and outflow. Because of long water retention times with only moderate to slight horizontal movements of water (e.g. longshore currents), vertical density stratification commonly occurs for both heat and chemicals. Hence, a distinct and stable vertical regime is established twice each year in dimictic lakes for various physical, chemical, and biological processes and substances. In addition to thermal and chemical stratification, both dissolved oxygen and pH levels have pronounced vertical profiles (e.g. Hutchinson 1957). Production processes, such as photosynthesis, at the autotrophic or primary production level generally take place in the upper trophogenic layer, while the lower, tropholytic layer may serve as a sink for organic matter produced in the upper zone (Wetzel 1975), as well as for heterotrophic activity. Hence, in general, the composite orientation and therefore, the organization of dimictic lakes of the north-temperate zone, appears to be based primarily on a vertical process and structural regime (Fig. 1B), rather than on the horizontal regime found in rivers (Vannote et al. 1980). Nonetheless, when the hyporheic zone and current velocity stratification are considered, rivers have an important vertical dimension as well.

Chemical contamination within a lake may not dissipate as rapidly as in rivers, but rather diminishes over comparably lengthy periods of time depending on internal rates of dilution. The acute effect, however, is usually localized, with lesser, often undetectable effects occurring remote from the spill over longer time periods. Bottom sediments and biota may both be expected to absorb and retain certain contaminant loads over lengthy periods of time, giving up part of their burden to the water column during each overturn.

While space–time considerations and horizontal–vertical organization are not exclusive properties of either rivers or lakes, it is apparent that rivers and river processes with their horizontal orientation, may be more readily analysed on a spatial basis, while lakes with largely vertical regimens and structures might best be addressed on a trend-through-time basis.

Exogenous and Endogenous Effects

As a generality, forces external to the system tend to directly influence rivers more than lakes (Fig. 1C), resulting in a more variable and unpredictable environment in the former instance (Sanders 1972). The morphology of rivers is subject to constant change through channel cutting, shore erosion and depositional processes. Weather has a large influence on water temperature, water levels, flow rates, and turbidity. As an example, stream water levels show instant response to summer rainstorms; however, an event of equal magnitude may have only imperceptible effects on lake levels.

Lakes in general, tend to have more stable properties over time, and much of this stability is derived from the buffering capacity of the biota. As the Gaia hypothesis (Lovelock 1979) presumes that life on earth controls atmospheric conditions such that they are optimal for the biosphere (and hence biota), so does life in a lake provide feedback to the environment which results in the homeostatic regulation of a benign and favorable milieu for aquatic organisms. Hence, biological buffering is more prevalent in lakes than in rivers.

Both rivers and lakes derive energy and nutrients from within and from outside their immediate channels or basins (Fig. 1D). The difference between these two aquatic systems is the relative proportion of nutrients and energy obtained from the two sources. Nutrient and energy sources, especially at the headwaters of a stream system, are largely allochthonous, that is, derived from allochthonous detritus (Hynes 1970); while for most lakes, autochthony, or internal recycling, constitutes the major source for both energy and nutrients (Hutchinson 1957). The level of autochthony achieved by any particular lake is related to its trophic status. Hence, eutrophic lakes are more dependent on allochthonous nutrient sources than are oligotrophic lakes.

While rivers and lakes constitute structurally different types of open systems, both are subjected to exogenous and endogenous effects to varying degrees including allochthonous and autochthonous sources of nutrients (Fig. 1D). However, all things being equal, rivers are more immediately responsive to exogenous effects than are lakes. Perhaps this derives from the fact that rivers are *more* of an open system than are lakes, or alternatively, that lakes are closer to being true microcosms than are rivers (Forbes 1887).

Abiotic and Biotic Influences

Rivers and lakes are subjected to different ecosystem controls derived from either abiotic or biotic sources (Fig. 1E). As previously noted, rivers are more influenced by the vagaries of weather, and over the long term, may be more closely attuned to climate than are lakes, especially thermally stratified, oligotrophic lakes. Rivers are also more responsive to their immediate geological and physiographic settings, and offer relatively little biologial buffering to these influences when compared with lakes. This effect for streams is variable from headwaters to mouth as biological buffering increases downstream. Abiotic effects are proportionally greater on eutrophic lakes than on oligotrophic lakes, the latter of which owe a greater proportion of their control to biotic effects. Extreme eutrophy, or hypereutrophy, has many of its biological processes curtailed because of the inordinately stressful nature of the abiotic effects (i.e. excessive phosphorous loadings).

The trophic cline in lakes, from oligotrophic to eutrophic, may also occur within a single river, normally with an augmentation of nutrients from headwaters to mouth. This gradual increase in the nutrient levels of a stream is not always predictable, as inflowing tributaries of substantially lower nutrient levels could dilute substantially the nutrient levels in the mainstream (e.g. Ryder 1964). Nonetheless, as a generality it may be said that a river is more buffered biologically as it is traversed in a downstream direction, while lakes may be more biologically buffered in time, through oligotrophication, a consequence of a loss of nutrients over time. It is also recognized that this process in lakes represents a counterpart process to the low-nutrient tributary flow into the mainstream of a river.

As previously noted, the ratio of heterotrophy to autotrophy (H/A) in rivers varies as they are traversed from headwaters to mouth (Fig. 1E). The highest H/A ratios occur in the shaded headwaters and the relatively turbid mouths of streams; there, solar insolation is reduced, and heterotrophic production becomes proportionately greater.

Lakes typically have the greatest levels of autotrophy in the upper trophogenic zone where solar light penetration is highest, and the lowest levels in the darker, tropholytic waters below. A more apt comparison with rivers on the basis of an H/A ratio may be made on a temporal scale for north-temperate lakes which have highest levels of photosynthesis during the long daylight hours of summer and lowest levels during the relatively short days of winter. The latter effect is accentuated through the presence of a thick layer of ice and snow over the surface of a lake at northerly latitudes. Accordingly, H/A ratios for lakes, will be lowest in summer and highest during winter (Fig. 1F).

Community Structure

The structure of river and lake communities differ considerably, both in time and spatially. Studies of low-order streams have demonstrated that biotic communities in temperate regions may form "a temporal sequence of synchronized species replacement" (Vannote et al. 1980), however, this is not necessarily true of equatorial regimes (Statzner and Higler 1985). When species replacement occurs, each new species essentially fills the same ecological role as its predecessor, but is better adapted to some seasonal change in the microhabitat. The ecological consequence is an equitable distribution of energy over time, and an attendant maximization of resource use. Additionally, stream communities change spatially from headwaters to mouth, which in the case of benthos, is apparently a size-related dependency between the organism and its detrital food (Vannote et al. 1980).

Culturally unperturbed lake communities, on the other hand, do not change markedly from season to season, although topological distortion of specific community compartments may occur with the addition of new cohorts. In general, lake communities tend to be more stable than stream communities over time, and variation occurs spatially rather than temporally. For example, it has been shown that percid communities have a habitat median of central tendency distinct from that of salmonid communities, even when both communities occur sympatrically in the same lake (Ryder and Kerr 1978). Usually one or more environmental parameters are sufficient for ecological separation of the two communities (e.g. Svärdson 1976); in the latter instance, temperature alone would seem to suffice, although phosphorous may also be important in this respect (Marshall and Ryan 1987).

On this basis then, community diversity might be expected to be highest in mesotrophic lakes where species from three distinct communities may find discrete areas of the lake best suited to their life requirements (Ryder and Kerr 1978; 1989). On a regional basis (the north-temperate zone, for example), maximum community diversity occurs in those medium to large lakes that combine the widest range of environmental conditions (Barbour and Brown 1974).

Similarly, maximum community diversity and primary production are generally greatest in streams of the third to fifth order, which are usually medium-sized streams occupying the mid-point of the sequence of stream order and having the widest range of temperature variation (Vannote et al. 1980; but see Statzner and Higler 1985).

Transferable Science and Research Needs

Certain aspects of lake ecology may be readily transferred to rivers to good advantage. Many phenomena that are temporal occurrences in lakes occur spatially in rivers from headwaters to mouth; where these are fundamental ecosystem or community properties, such as production or diversity, appropriate insights may be gained from lake data sets for rivers within the same climatic zone. In fact, space-time axes may be profitably interchanged between rivers and lakes for various measurements, and in many applications. Application of ergodic theory (Ryder et al. 1974), that is, relating the means of temporal strings with those of spatial arrays, may be one approach useful for utilizing lake information within a river context. Such an approach for biologists would allow rapid transfer of ecological insights from lakes to rivers. It may also provide a directionality for future research on rivers, or at least be indicative of research needs.

In the latter area, the pragmatic need that is foremost is the development of an ecologically sound, conceptual basis for the estimation of standing stocks and production of fishes in rivers (Welcomme et al. 1989). An urgent requirement is to be timely with these estimates, rather than place an overemphasis on precision (e.g. Henderson et al. 1973). Accordingly, the development of a fish yield estimator for streams on the same order of precision as the morphoedaphic index for lakes (Ryder et al. 1974), would be a first step towards the effective management of river systems.

Because fish productivity in streams is so closely linked with the bordering terrestrial environment (Hynes 1963), an awareness of both the former presettlement conditions (Minshall et al. 1985) and appropriate conservation strategies for riparian zones and watersheds would be an additional asset to stream management.

Finally, despite our attempts to show where science may be transferred from lakes to rivers in a practical and meaningful manner, it should not be assumed that the transfer will be easily implemented without the appropriate background studies. Throughout this paper we have noted the commonalities of rivers and lakes, but we have also emphasized the importance of qualitative differences (Table 8). When all is said and done, a river exceeds the simple description of "a mobile lake", and a lake is something more than a "river reach, frozen in time". In dealing with these qualitative differences between rivers and lakes, much remains to be done.

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References

Adams, C. C. 1901. Baseleveling and its faunal significance with illustrations from southeastern United States. Am. Nat. 35: 839–852.

Alexander, R. M. 1967. Functional design in fishes. Hutchinson Lib., London. 160 p.

Ambühl, H. 1961. Die Strömung als physiologischer und ökologischer Faktor. Experimentelle Untersuchungen an Bachtieren. Verh. Int. Ver. Limnol. 14: 390–395.

Bagenal, T. [ed.] 1978. Methods for assessment of fish production in fresh waters. IBP Handbook No. 3, Blackwell Sci. Pub., London. 365 p.

Balon, E. K., W. T. Momot, and H. A. Regier. 1977. Reproductive guilds of percids: results of the paleogeographical history and ecological succession. J. Fish. Res. Board Can. 34: 1910–1921.

Barbour, C. D., and J. H. Brown. 1974. Fish species diversity in lakes. Am. Nat. 108: 473–489.

Barton, D. R., W. D. Taylor, and R. M. Biette. 1985. Dimensions of riparian buffer strips required to maintain trout habitat in southern Ontario streams. N. Am. J. Fish. Manage. 5: 364–378.

Beaumont, P. 1975. Hydrology, p. 1–38. *In* B. A. Whitton [ed.] River ecology. University of California Press, Berkely, Ca.

Benfield, E. F. 1981. Primary production in stream ecosystems, p. 82–90. *In* L. A. Krumholz [ed.] Warmwater Streams Symposium. Allen Press, Lawrence, KS.

Blum, J. L. 1972. Plant ecology in flowing water, p. 53–56. *In* R. T. Oglesby, C. A. Carlson, and J. A. McCann [ed.] River ecology and man. Academic Press, New York, NY.

Borner, L. 1917. Die Bodenfauna des St. Moritzer — See. Inaugural Dissertation. Basel. Univ. Stuttgart. 163 p.

Brett, J. R., and D. F. Alderdice. 1958. The resistance of cultured young chum and sockeye salmon to temperatures below 0° C. J. Fish. Res. Board Can. 15: 805–813.

Brinkhurst, R. O. 1974. Benthos in lakes. MacMillen, Toronto, Ont. 190 p.

Brown, G. W. 1969. Predicting temperatures of small streams. Wat. Resour. Res. 5: 68–75.

Cairns, J., Jr. 1968. Suspended solids standard for the protection of aquatic organisms. Purdue Univ. Engin. Bull. 129: 16–27.

Cordone, A. J., and D. W. Kelly. 1961. The influence of inorganic sediment on the aquatic life of streams. Calif. Fish. Game 47: 189–228.

Cummins, K. W. 1972. What is a river? — A zoological description, p. 33–52. *In* R. T. Oglesby, C. A. Carlson, and J. A. McCann [ed.] River ecology and man. Academic Press, New York, NY.

1974. Structure and function of stream ecosystems. Bioscience 24: 631–641.

1975. The importance of different energy sources in freshwater ecosystems, p. 50–54. *In* Productivity of world ecosystems. Proc. Symp. Aug. 31–Sept. 1, 1972. National Academy of Science, Washington, DC.

1977. From headwater streams to rivers. Amer. Biol. Teach. 39: 305–312.

Cummins, K. W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. Ann. Rev. Ecol. Syst. 10: 147–172.

Cummins, K. W., and G. L. Spengler. 1978. Stream ecosystems. Water Spectrum Fall: 1–9.

Cummins, K. W., G. W. Minshall, J. R. Sedell, C. E. Cushing, and R. C. Peterson. 1984. Stream ecosystem theory. Verh. Int. Ver. Limnol. 22: 1818–1827.

Cushing, C. E. 1966. Periphyton productivity and radionuclide accumulation in the Columbia River, Washington, U.S.A. Hydrobiol. 29: 125–139.

Cushing, C. E., C. D. McIntire, K. W. Cummins, G. W. Minshall, R. C. Petersen, J. R. Sedell, and R. L. Vannote. 1983. Relationships among chemical, physical, and biological indices along river continua based on multivariate analyses. Arch. Hydrobiol. 98: 317–326.

Dillon, P. J., and F. H. Rigler. 1975. A simple method for predicting the capacity of a lake for development based on lake trophic status. J. Fish. Res. Board Can. 32: 1519–1531.

Ellis, M. M. 1936. Erosion silt as a factor in aquatic environments. Ecology 17: 29–42.

Fernando, C. H. 1980. Tropical man-made lakes, African fish and cheap protein. ICLARM Newsletter 3(1): 15–17.

Forbes, S. T. 1887. The lake as a microcosm. Bull. Peoria Sci. Assoc. 1887: 77–87.

Francis, G. R., A. P. L. Grima, H. A. Regier, and T. H. Whillans. 1985. A prospectus for the management of the Long Point ecosystem. Great Lakes Fish. Comm., Tech. Rep. No. 43: 1–109.

Gammon, J. R., and J. M. Reidy. 1981. The role of tributaries during an episode of low dissolved oxygen in the Wabash River, Indiana, p. 396–407. *In* L. A. Krumholz [ed.] The Warmwater Streams Symposium. Allen Press, Lawrence, KS.

Gibbs, R. J. 1970. Mechanisms controlling world water chemistry. Science 170: 1088–1090.

Greenbank, J. 1945. Limnological conditions in ice-covered lakes, especially as related to winter-kill of fish. Ecol. Monogr. 15: 344–392.

Grossman, G. D., P. B. Moyle, and J. O. Whittaker, Jr. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. Am. Nat. 120: 423–454.

Haslam, S. M. 1978. River plants (the macrophytic vegetation of water-courses). Combridge University Press, New York, NY. 396 p.

Hawkes, H. A. 1975. River zonation and classification, p. 312–374. *In* B. A. Whitton [ed.] River Ecology. Studies in Ecology, Vol. 2, Univ. California Press, Berkeley, CA.

Hayes, F. R. 1957. On the variation in bottom fauna and fish yield in relation to trophic level and lake dimensions. J. Fish. Res. Board Can. 14: 1–32.

Henderson, H. F., R. A. Ryder, and A. W. Kudhongania. 1973. Assessing fishery potentials of lakes and reservoirs. J. Fish. Res. Board Can. 30: 2000–2009.

Hocutt, C. H., and J. R. Stauffer. 1975. Influence of gradient on the distribution of fishes in Conowingo Creek, Maryland and Pennsylvania. Chesapeake Sci. 16: 143–147.

Holling, C. S. 1985. Resilience of ecosystems: local surprise and global change, p. 228–269. *In* T. F. Malone and J. G. Roederer [ed.] Proc. Symp. ICSU, 20th Gen. Assembly. Cambridge University Press, London.

Horton, R. E. 1945. Erosional development of streams and their drainage basins: hydrophysical approach to quantitative morphology. Bull. Geol. Soc. Am. 56: 275–370.

Huet, M. 1946. Note preliminaire sur les relations entre la pente et les populations piscicoles des eaux courantes. Règle des pentes. 13^{e} Biologisch Jaarboek, Dodanaea, Bruxelles, p. 232–243.

1949. Aperçu des relations entre la pente et les populations piscicoles des eaux courantes. Rev. Suiss Hydrol. 11: 323–351.

1959. Profiles and biology of western European streams as related to fish management. Trans. Am. Fish. Soc. 3: 155–163.

Hughes, R. M., and J. M. Omernik. 1981. Use and misuse of the terms watershed and stream order, p. 320–326. *In* L. A.

Krumholz [ed.] Warmwater Streams Symposium. Allen Press, Lawrence, KS.

Hunt, R. L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. J. Fish. Res. Board Can. 26: 1473–1483.

Hutchinson, G. 1957. A treatise on limnology. Vol. 1. John Wiley and Sons, New York, NY. 1015 p.

Hutchinson, G. E. 1961. The paradox of the plankton. Am. Nat. 95: 137–145.

1975. A treatise on limnology. Vol. III. John Wiley and Sons, New York, NY. 660 p.

Hynes, H. B. N. 1963. Imported organic matter and secondary productivity in streams. Proc. XVI Int. Congr. Zool. 4: 324–329.

1970. The ecology of running waters. University of Toronto Press, Toronto, Ont. 555 p.

1975. The stream and its valley. Verh. Int. Ver. Limnol. 19: 1–15.

Iwamoto, R. N., E. O. Salo, M. A. Madej and R. L. McComas. 1978. Sediment and water quality: a review of the literature including suggested approach for water quality criteria. U. S. Environ. Prot. Agency EPA 910/9-78-048 Washington, DC.

Kerekes, J. 1976. Index of lake basin permanence. Int. Rev. Gesamten Hydrobiol. 62: 291–293.

Kitchell, J. F., M. S. Johnson, C. K. Minns, K. H. Loftus, L. Greig, and C. H. Olver. 1977. Percid habitat: the river analogy. J. Fish. Res. Board Can. 34: 1936–1940.

Kuehne, R. A., and R. W. Barbour. 1983. The American Darters. Kentucky Univ. Press, Lexington, Kentucky. 177 p.

Kuhn, T. S. 1962. The structure of scientific revolutions. Foundations of the Unity of Sci. 11: 1–210.

Larimore, R. W. 1981. Progress and challenges of the fishery biologist in warmwater stream investigations, p. 120–126. *In* L. A. Krumholz [ed.] Warmwater Streams Symposium. Allen Press, Lawrence, KS.

Leopold, L. B. 1953. Downstream change of velocity in rivers. Am. J. Sci. 251: 606–624.

Leopold, L. B., M. B. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. Freeman, San Francisco, CA.

Lissman, H. W. 1963. Electric location in fishes. Sci. Am. 152: 1–12.

Lovelock, J. E. 1979. Gaia: a new look at life on Earth. Oxford University Press, Oxford.

MacArthur, R. H. 1972. Geographical ecology. Harper and Row, New York, NY. 269 p.

Maciolek, J. A., and P. R. Needham. 1951. Ecological effects of winter conditions on trout and trout foods in Convict Creek, California, 1951. Trans. Am. Fish. Soc. 81: 202–217.

Margalef, R. 1960. Ideas for a synthetic approach to the ecology of running waters. Int. Rev. Gesamten Hydrobiol. 45: 133–153.

Marshall, T. R., and P. A. Ryan. 1987. Abundance patterns and community attributes of fishes relative to environmental gradients. Can. J. Fish. Aquat. Sci. 44 (Suppl. 2): 198–215.

Martin, N. V. 1957. Reproduction of lake trout in Algonquin Park, Ontario. Trans. Am. Fish. Soc. 86: 231–244.

McCombie, A. M. 1959. Some relations between air temperatures and the surface water temperature of lakes. Limnol. Oceanogr. 4: 252–258.

McIntire, C. D. 1975. Periphyton assemblages in laboratory streams, p. 403–430. *In* B. A. Whitton [ed.] River ecology. Univ. California Press, Los Angeles, CA.

Milbrink, G. 1969. Microgradients at the mud–water interface. Inst. Freshw. Res., Drottningholm 49: 129–148.

Minckley, W. L. 1963. The ecology of a spring stream Doe Run, Meade County, Kentucky. Wildl. Monogr. 11: 1–124.

Minshall, G. W., K. W. Cummins, R. C. Petersen, C. E. Cushing, D. A. Bruns, J. R. Sedell, and R. L. Vannote. 1985. Developments in stream ecosystem theory. Can. J. Fish. Aquat. Sci. 42: 1045–1055.

Moon, H. P. 1939. Aspects of the ecology of aquatic insects. Trans. Br. Entomol. Soc. 6: 39–49.

Moore, G. A. 1944. The retinae of two North American teleosts, with special reference to their tapeta lucida. J. Somp. Neur. 80: 369–379.

Mortimer, C. H. 1971. Chemical exchanges between sediments and water in the Great Lakes — speculations on probable regulatory mechanisms. Limnol. Oceanogr. 16: 387–404.

Moss, B. 1980. Ecology of fresh waters. John Wiley and Sons, Toronto, Ont. 332 p.

Moyle, P. B., and J. J. Cech, Jr. 1982. Fishes: An introduction to ichthyology. Prentice-Hall, Inc., Englewood Cliffs, NJ. 593 p.

Müller, K. 1974. Stream drift as a chronobiological phenomenon in running water ecosystems. Ann. Rev. Ecol. Syst. 5: 309–323.

Neel, J. K. 1951. Interrelations of certain physical and chemical features in a headwater limestone stream. Ecology 32: 368–391.

Nelson, D. J., and C. C. Scott. 1962. Role of detritus in the productivity of a rock-outcrop community in a Piedmont stream. Limnol. Oceanogr. 3: 396–413.

Nelson, J. S. 1976. Fishes of the World. John Wiley and Sons, New York, NY. 416 p.

Odum, E. P. 1971. Fundamentals of ecology. W. B. Saunders Company, Philadelphia, PA. 574 p.

Odum, H. 1956. Primary production in flowing waters. Limnol. Oceanogr. 1: 102–117.

Orghidan, T. 1959. Ein neuer Lebensraum des unterirdischen Wassers: Der hyporheische Biotop. Arch. Hydrobiol. 55: 392–414.

Patrick, R. 1972. Commentary, p. 67–74. *In* R. T. Oglesby, C. A. Carlson and J. A. McCann [ed.] River ecology and man. Academic Press, New York, NY.

Pennak, R. W. 1978. Fresh-water invertebrates of the United States (Second Edition). John Wiley and Sons, Toronto, Ont. 803 p.

Pennak, R. W., and J. V. Ward. 1986. Interstitial faunal communities of the hyporheic and adjacent groundwater biotopes of a Colorado mountain stream. Arch. Hydrobiol. Suppl. 74: 356–396.

Platts, W. S. 1979. Relationships among stream order, fish populations, and aquatic geomorphology in an Idaho River drainage. Fisheries 2: 5–9.

Platts, W. S., W. F. Megahan, and G. W. Minshall. 1983. Methods for evaluating stream, riparian and biotic conditions. Gen. Tech. Rep. INT-138. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 1983. 70 p.

Pugsley, C. W., and H. B. N. Hynes. 1986. Three-dimensional distribution of winter stonefly nymphs, *Allocapnia pygmaea*, within the substrate of a southern Ontario river. Can. J. Fish. Aquat. Sci. 43: 1812–1817.

Rawson, D. S. 1952. Mean depth and the fish production of large lakes. Ecology 33: 513–521.

1953. The bottom fauna of Great Slave Lake. J. Fish. Res. Board Can. 10: 487–520.

1960. A limnological comparison of twelve large lakes in northern Saskatchewan. Limnol. Oceanogr. 5: 195–211.

Regier, H. A., and H. F. Henderson. 1980. Comparative studies on fresh-water fisheries. FAO Fish. Tech. Pap. No. 198: 46 p.

Reid, G. K. 1961. Ecology of inland waters and estuaries. Reinhold Publishing Corporation, New York, NY. 375 p.

Reimers, N. 1963. Body condition, water temperature, and overwinter survival of hatchery-reared trout in Convict Creek, California. Trans. Am. Fish. Soc. 92: 39–45.

RICKER, W. E. 1934. An ecological classification of certain Ontario streams. Publ. Ont. Fish. Res. Lab. No. 49: 1–114.

1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

RYAN, P. A., AND T. R. MARSHALL, [in prep.]. Towards a definition of the lake trout (*Salvelinus namaycush*) niche through indices of environmental quality.

RYCK, F., JR. 1975. The effect of scouring floods on the benthos of Big Buffalo Creek, Missouri. Proc. 29th Ann. Conf. Southeast. Assoc. Game Fish Comm. 29: 36–45.

RYDER, R. A. 1964. Chemical characteristics of Ontario lakes as related to glacial history. Trans. Am. Fish. Soc. 93: 260–268.

1977. Effects of ambient light variations on behavior of yearling, subadult, and adult walleyes (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34: 1481–1491.

1978a. Ecological heterogeneity between north-temperate reservoirs and glacial lake systems due to differing succession rates and cultural uses. Verh. Int. Ver. Limnol. 20: 1568–1574.

1978b. Fish yield assessment of large lakes and reservoirs — a prelude to management, p. 403–423. *In* S. D. Gerking [ed.] Ecology of Freshwater Fish Production. John Wiley and Sons, New York, NY.

RYDER, R. A., AND S. R. KERR. 1978. The adult walleye in the percid community — a niche definition based on feeding behavior and food specificity, p. 39–51. *In* R. L. Kendall [ed.] Selected coolwater fishes of North America. Am. Fish. Soc. Spec. Pub. No. 11: 1–437.

1988. Harmonic communities in aquatic ecosystems: a management perspective. *In* R. W. Welcomme [ed.] Symposium on management schemes for inland fisheries. European Inland Fisheries Advisory Commission (EIFAC) XV/88/Symp.1. Goteborg, Sweden.

RYDER, R. A., S. R. KERR, K. H. LOFTUS, AND H. A. REGIER. 1974. The morphoedaphic index, a fish yield estimator — review and evaluation. J. Fish. Res. Board Can. 31: 663–688.

SANDERS, W. M., III. 1972. Nutrients, p. 389–415. *In* R. T. Oglesby, C. A. Carlson, and J. A. McCann [ed.] River ecology and man. Academic Press, New York, NY.

SCHINDLER, D. W. 1977. Evaluation of phosphorus limitation in lakes. Science 195: 260–262.

SCHINDLER, D. W., AND J. E. NIGHSWANDER. 1970. Nutrient supply and primary production in Clear Lake, eastern Ontario. J. Fish. Res. Board Can. 27: 2009–2036.

SCHLOSSER, I. J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. Ecology 66: 1484–1490.

SCHMITZ, W. 1954. Grundlagen der Untersuchung der Temperaturverhältnisse in den Fliessegewässern. Berl. Limnol. Flusstat. Freudenthal 6: 29–50.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

SEDELL, J. R., AND J. L. FROGGATT. 1984. Importance of streamside forests to larger rivers: the isolation of the Willamette River, Oregon, U.S.A. from its flood plain by snagging and streamside forest removal. Verh. Int. Ver. Limnol. 22: 1828–1834.

SEDELL, J. R., J. E. RICHEY, and F. J. SWANSON. 1989. The river continuum concept: a basis for the expected ecosystem behavior of very large rivers?, p. 49–55. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

SHELFORD, V. E. 1914. An experimental study of the behaviour agreement among animals of an animal community. Biol. Bull. 26: 294–315.

SHELFORD, V. E., AND S. EDDY. 1929. Methods for the study of stream communities. Ecology 10: 383–392.

SMITH, R. L. 1980. Ecology and field biology (3rd ed.). Harper and Row, New York, NY. 835 p.

SPEAKER, R., K. MOORE, AND S. GREGORY. 1984. Analysis of the process of retention of organic matter in stream ecosystems. Verh. Int. Ver. Limnol. 22: 1835–1841.

SPRULES, W. M. 1952. The Arctic char on the west coast of Hudson Bay. J. Fish. Res. Board Can. 9: 1–15.

STANFORD, J. A., AND A. R. GAUFIN. 1974. Hyporheic communities of two Montana rivers. Science 185: 700–702.

STATZNER, B., AND B. HIGLER. 1985. Questions and comments on the River Continuum Concept. Can. J. Fish. Aquat. Sci. 42: 1038–1044.

STRAHLER, A. N. 1957. Quantitative analysis of watershed morphology. Trans. Am. Geophys. Union. 38: 913–920.

STUMM, W., AND J. J. MORGAN. 1970. Aquatic chemistry — an introduction emphasizing chemical equilibria in natural waters. Wiley-Interscience, Toronto, Ont. 583 p.

SUMNER, W. T., AND S. G. FISHER. 1979. Periphyton production in Fort River, Massachusetts. Freshwat. Biol. 9: 205–212.

SVÄRDSON, G. 1976. Interspecific population dominance in fish communities of Scandinavian lakes. Inst. Freshw. Res., Drottningholm, Rep. No. 55: 144–171.

THIENEMANN, A. 1953. Fluss und See, ein limnologischer Vergleich. Gewaesser und Abwaesser 1: 13–30.

TRISKA, F. J. 1984. Role of wood debris in modifying channel geomorphology and riparian areas of a large lowland river under pristine conditions: a historical case study. Verh. Int. Ver. Limnol. 22: 1876–1892.

VALLENTYNE, J. R. 1972. Freshwater supplies and pollution: effects of the demophoric explosion on water and man, p. 181–211. *In* N. Polunin [ed.] The environmental future. Macmillan Press, London.

VAN DOBBEN, W. H., AND R. H. LOWE-MCCONNELL [ed.]. 1975. Unifying concepts in ecology. First Int. Congr. Ecol., The Hague, the Netherlands. 302 p.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

VARLEY, M. E. 1967. British freshwater fishes (factors affecting their distribution). Fishing News (Books) Limited. London, England. 148 p.

WALLACE, J. B., J. R. WEBSTER, AND W. R. WOODALL. 1977. The role of filter feeders in flowing waters. Arch. Hydrobiol. 79: 506–532.

WALLEN, I. E. 1951. The direct effect of turbidity on fishes. Oklahoma Agri. Mech. Coll. Biol. Ser. 48: 1–27.

WARD, J. V. 1985. Thermal characteristics of running waters. Hydrobiol. 125: 31–46.

1986. Attitudinal zonation in a Rocky Mountain stream. Arch. Hydrobiol. Suppl. 74: 133–199.

WARD, J. V., AND J. A. STANFORD. 1989. Riverine ecosystems: the influence of man on catchment dynamics and fish ecology, p. 56-64. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Pub. Fish. Aquat. Sci. 104.

WATERS, T. F. 1969. Invertebrate drift-ecology and significance to stream fishes, p. 121–134. *In* T. G. Northcote [ed.] Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fish., Inst. Fish., Univ. British Columbia, Vancouver, BC.

WEBSTER, J. R. 1975. Analysis of potassium and calcium dynamics in stream ecosystems on three southern Appalachian watersheds of contrasting vegetation. Ph.D. Dissertation. University of Georgia, Athens, GA. 232 p.

WELCH, P. S. 1952. Limnology. McGraw-Hill Co., Toronto, Ont. 538 p.

Welcomme, R. L. 1976. Some general and theoretical considerations on the fish yield of African rivers. J. Fish. Biol. 8: 351–364.

1979. Fisheries ecology of flood plain rivers. Longman Group Ltd., London. 317 p.

1985. River fisheries. FAO Fisheries Tech. Pap. 262: 330 p.

1989. Review of the present state of knowledge of fish stocks and fisheries of African rivers, p. 515–532. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Pub. Fish. Aquat. Sci. 106.

Welcomme, R. L., R. A. Ryder, and J. R. Sedell. 1989. Dynamics of fish assemblages in river systems — a synthesis, p. 569–577. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Pub. Fish. Aquat. Sci. 106.

Wetzel, R. G. 1975. Limnology. W. B. Saunders Co., Philadelphia, PA. 743 p.

Whitford, L. A., and G. J. Schumacher. 1961. Effect of current on mineral uptake and respiration by a fresh-water alga. Limnol. Oceanogr. 6: 423–425.

Winger, P. V. 1981. Physical and chemical characteristics of warmwater streams: a review, p. 32–44. *In* L. A. Krumholz [ed.] Warmwater streams symposium. Allen Press, Lawrence, KS.

Wright, R. R. 1892. Preliminary report on the fish and fisheries of Ontario. Ont. Game Fish. Comm., Toronto, Ont. p. 421–428.

Yakuwa, I. 1960. Phase of the diurnal variation of water temperature of a river. Mem. Enging. Fac. Hokkaido Univ. 11: 1–10.

Rehabilitation of Degraded River Ecosystems

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Abstract

Regier, H.A., R.L. Welcomme, R.J. Steedman, and H.F. Henderson. 1989. Rehabilitation of degraded river ecosystems, p. 86–97. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Through carelessness, misunderstanding, or ignorance of ecosystem properties, riverine ecosystems have often been degraded unnecessarily, especially in developed countries. Efforts are intensifying to forestall degradation where economic development is occurring and to undertake rehabilitation where degradation has occurred.

Ecodevelopment of pristine rivers and sustainable redevelopment of degraded rivers is intended to result in more harmonious and productive human/nature ecosystems. Conventional environmental and resource sciences in their present states are poorly suited for this challenge. A more appropriate scientific approach to river rehabilitation may emerge from a synthesis of recent work on historical ecology, ecosystem development and empirical generalizations from comparative studies of river ecosystems.

Here we take an ecosystem approach with a focus on self-organizing ecosystem properties that lead to the production of highly valued products and features. Conventional development causes ecosystemic disorganization and often cripples self-organizing capabilities. Rehabilitation should correct the causes of disorganization and crippling, and should foster recovery.

Résumé

Regier, H.A., R.L. Welcomme, R.J. Steedman, and H.F. Henderson. 1989. Rehabilitation of degraded river ecosystems, p. 86–97. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

A cause de la négligence, par malentendu ou ignorance des propriétés des écosystèmes, les écosystèmes fluviaux ont été inutilement dégradés surtout dans les pays industrialisés. De plus grands efforts sont déployés afin de prévenir la dégradation là où s'effectue un développement économique et d'entreprendre la réhabilitation des écosystèmes dégradés.

L'écodéveloppement de cours d'eau vierges et le redéveloppement soutenu de cours d'eau dégradés visent la création d'écosystèmes plus harmonieux et plus productifs au niveau homme/nature. Dans leurs états actuels, les sciences traditionnelles traitant de l'environnement et des ressources sont pauvrement adaptées à ce défi. Une synthèse des travaux récents sur l'écologie historique, le développement des écosystèmes et les généralisations empiriques tirées d'études comparatives d'écosystèmes fluviaux pourrait donner naissance à une approche scientifique plus appropriée à la réhabilitation des cours d'eau.

Dans la présente étude, les auteurs abordent le problème par la théorie de l'écosystème en se concentrant sur ses propriétés d'auto-organisation qui mènent à l'élaboration de produits et de caractéristiques très recherchés. Le développement traditionnel entraîne la désorganisation des écosystèmes et paralyse souvent les capacités d'auto-organisation. La réhabilitation devrait corriger ces problèmes et favoriser le rétablissement.

Introduction

A river system degraded by humans has been rendered less productive of valued natural features present originally, and has been made more productive of unpleasant and harmful features. Some of the unpleasant features may be new and others may be old but intensifed. Rehabilitation, along with 14 other options for the management of large river ecosystems, is defined as in Table 1 (modified from Regier et al. 1980).

There is a large body of literature on rivers that are under the influence of particular human uses and abuses, especially with regard to rivers that are not severely degraded. There is far less literature on rivers in either a primeval natural state or in a severely degraded state. There are few case studies that describe and explain in an ecological context precisely how and why a river has been altered by humans (but see Karr et al. 1985; Bravard et al. 1986; Hesse 1987). Interest in mitigation, restoration, remediation, and rehabilitation has been growing in recent years, and many efforts along these lines have been undertaken, usually on a trial-and-error basis. In our paper we try to identify concepts and information sources appropriate to understanding organizational transformations of large river ecosystems under human influence.

TABLE 1. Fifteen political options for the management of ecosystems, such as a river or river basin.

1. Preservation of locales of wild nature in a primeval state.
2. Restoration of despoiled features of nature to the original primeval state. (Many authors use restoration for what we have termed rehabilitation, see below.)
3. Melioration or enhancement of parts of the existing ecosystem by infusing desirable new ecological features that were not present in the primeval state, but are generally compatible with nature.
4. Optimization of one or more human uses of the ecosystem with each use practiced in an ecologically sensitive way. (Many authors use the term conservation for this option).
5. Mitigation of undesired impacts of conventional human practices on ecosystems by creation of a new desirable feature that compensates for an old desirable feature that is sacrificed.
6. Remediation by reducing the intensity of one or more human abuses.
7. Rehabilitation of a river or river basin through a judicious mix of the six options listed above.
8. Reclamation by redirecting major natural processes for some particular human use, such as dewatering a wetland. (Many authors use the term reclamation for what we have termed rehabilitation here, see above.)
9. Commercialization by transforming natural features and products for sale.
10. Urbanization by developing dense human settlements in the ecosystem.
11. Industrialization by siting major enterprises, inevitably with ecological impact, in the ecosystem.
12. Palliation by using other scarce resources ostensibly to protect nature, but only by token or ineffective means.
13. Pollution through externalization of useless or harmful by products of human activities to be diluted, inactivated or assimilated by the natural parts of the ecosystem.
14. Degradation by ignoring or despoiling wild nature, carelessly or for some developmental or military end.
15. Abiotization or sterilization by eradicating much of nature and creating a development that might consist almost entirely of non-living or "abiotic" structures of concrete, glass, steel, and similar man-made materials; biota that remain include humans, their pathogens and pets, certain birds, mammals and fish, most of which are non-indigenous.

Transformations of Large River Ecosystems

Development and Redevelopment

Figure 1 provides a broad context into which rehabilitation initiatives may be fitted. Note that "rehabilitation" includes some or all of: preservation, restoration, melioration, conservation, mitigation, and remediation (Table 1).

Two major processes of natural resource use by humans are sketched in Fig. 1: conventional exploitative development (CED), and ecodevelopment (ED), or reform sustainable redevelopment (RSR). CED has been the dominant cultural process worldwide concerning the natural environment and renewable resources. Table 2 provides a characterization of an endpoint to the CED sequence as it relates to river ecosystems.

Ecodevelopment as a broad strategy was urged by the United Nations Environment Programme starting about 1974. In undeveloped regions it started implicitly from a conceptualization of a relatively natural and not seriously degraded state and then was intended to progress toward a desirable state of man–nature accommodation. Some early approximations to ED are becoming apparent in the planning functions in some underdeveloped countries. Agencies that grant international aid are beginning to pay more than mere lip service to these concepts. FAO in particular has incorporated ED concepts into its current plans and priorities. Some of the guidelines accepted at the FAO World Conference on Fisheries Management held in Rome, June

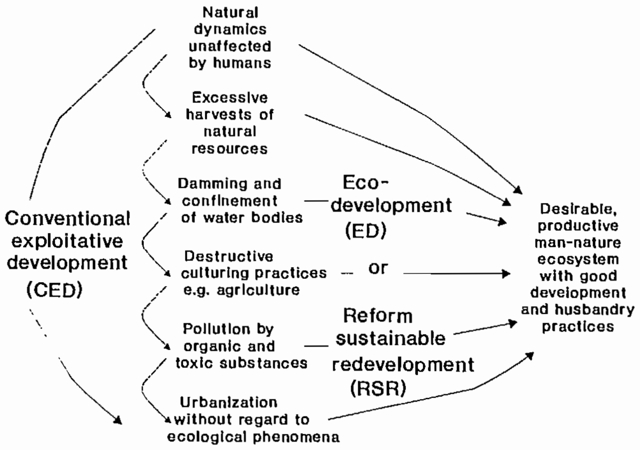


FIG. 1. Schema illustrating the meaning of conventional exploitative development, ecodevelopment, and reform sustainable redevelopment.

TABLE 2. Features of the general stress syndrome in aquatic systems, especially as related to fish and fisheries (as modified from Francis et al. 1985 and Rapport et al. 1985).

- Major stresses, due to human uses, often act synergistically so as to exacerbate each other's adverse effects. Stresses seldom act antagonistically so as to cancel out adverse effects.
- Stresses alter the fish association form one that is dominated by large fish usually associated with larger streams, with the lake bottom and lake edge to one characterized by small mid-water species or by tolerant back-water species. A similar change happens with respect to vegetation: firm rooted aquatic plants near shore originally are replaced by dense suspensions of open-water plankton algae or filamentous algae in shallow areas. In addition, the association of relatively large invertebrates such as mussels, crayfish and mayflies that live directly on bottom substrates is supplanted by an association characterized by small burrowing insects and worms such as midge larvae and sludge worms.
- With the above changes comes an increased variability from year to year in abundance of particular species, and in particular in landings of different fish species by anglers and commercial fishermen.
- The shift from large organisms associated with the bottom to small organisms in the bottom and in mid-water or to species of the back-waters is not accompanied by a great increase in the total biomass of living material, at least not of marketable species.
- Market and sport value per unit biomass is generally much lower with small mid-water fish species and back-water species than with large bottom species, and processing costs are higher. Similarly, the aesthetic value of the rooted plants near shore with the associated animals is higher than a pea-soup-like mixture of suspended algae or swaths of decaying filamentous algae and mats of sewage fungus.
- The effect on fisheries is that labor-intensive specialized fisheries (sport and commercial) tend to disappear, though mechanized, capital-intensive enterprises may persist if the combined stresses do not become excessive and if the fish are not so contaminated as to become a health threat for those who would eat them. Beyond that, people generally find such degraded systems offensive and quite literally turn their backs to them.

27 - July 6, 1984, (FAO 1985) may be mentioned: "Plans must include protection of aquatic habitats threatened by degradation" (I.xvii); "Governments must control pollution and maintain critical coastal ecosystems such as mangroves" (III.x); and "The development of [small scale] fishing should be part of integrated rural development" (IV.i).

Reform sustainable redevelopment is here viewed as consistent with ecodevelopment. RSR involves efforts to undo the excesses and harm of CED and to replace its bad practices with good practices like those of ED. Early beginnings of RSR may be apparent in some ecological recovery of British rivers and of rivers and lakes of the Laurentian Great Lakes Basin. In the Great Lakes Basin, expenditures totalling well over 10^{10} U.S. dollars (in 1987 equivalents) have been made since 1970 in attempts to remediate the abuses of CED and to rehabilitate the fisheries. RSR requires much more than tinkering with simplistic "retrofixes".

Much of the practical content of the case histories of rivers in this Symposium relates to phenomena generated within the CED sequence. Many attempts have been made to alter plans to ensure that the consequences are less degrading, to reduce the intensity of abuses, to compensate for some of the adverse consequences of CED, etc. All of these have an effect of deflecting the trajectory of the CED process away from an obnoxious end-state of ecological degradation and in the direction of a more desirable state.

But what the general features of a desirable end-state of ED and RSR should be is seldom addressed explicitly. We seem not to have progressed in our thinking beyond a form of ecodevelopment that shuns some of the most flagrant abuses of conventional exploitative development — not yet to a kind of reform sustainable redevelopment that involves more than incremental and ad hoc corrections of some CED abuses.

For an end-point of ED and RSR we propose some considerations:

- — Major self-regulatory ecosystemic processes and information networks should be protected if they still exist, or should be restored if they have been inactivated;
- — Locales or key structures related to ecosystemic sustainability and self-regulation, i.e. centres of organization (Steedman and Regier 1987), should be protected if they still exist, or should be restored if they have been destroyed;
- — Large biota that integrate structures and processes in ecosystemic self-regulation should be husbanded, and allowed freedom of movement;
- — Rivers, lakes, lagoons and wetlands should not be viewed merely as inert abiotic features, but should be seen as parts of a living ecosystem with a right to their own living space in which they have some geomorphological freedom to maintain dynamic structure; and
- — Valued ecosystem components should be used or exploited in moderation, especially since they are often integrally involved with the preceding considerations.

We should not presume to think that we can manage large river ecosystems; we may be able only to manage human uses of these ecosystems.

Stages in Ecosystemic Transformation

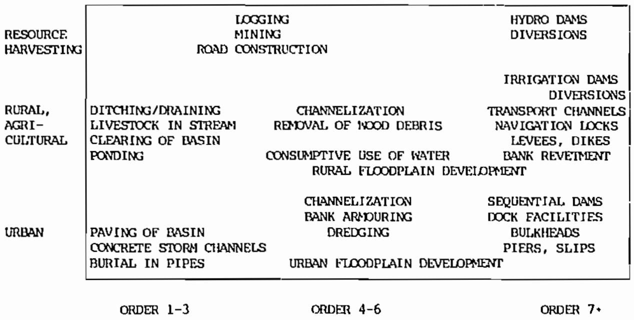
Consider large river systems in the context of the drainage basin and associated structural components including: the dendritic network of tributaries; the mainstem of the river; the floodplain including oxbow lakes, side channels and backwaters; the delta, estuary and bay including lagoons and distributaries; and nearshore parts of the receiving waterbody.

Five general categories of natural and unnatural stresses may be identified as affecting river ecosystems (Table 3). In severely degraded systems, all of these are likely to have been involved in some part of the degradation sequence (Fig. 1). A sixth category, climate change through the greenhouse effect, may soon be added (Meisner et al. 1987).

Degradative influences on running waters subjected to CED may be arranged simplistically along dimensions of river size and intensity of resource use (Fig. 2). In general CED acts to isolate a river from its watershed, primarily by inactivating the biotic connections between a river system and the riparian component of the watershed. The nature of river systems dictates that the form of this inactivation or decoupling is different between small streams and large rivers.

TABLE 3. A taxonomy of stresses that affect river ecosystems.

Natural background processes	Battering storms; rains and floods; water level cycles; spells of hot or cold weather; forest and marsh fires; disease outbreaks among key species; climate changes.
Harvesting of renewable resources	Fishing whether artisanal, commercial or angler; hunting for ungulates or waterfowl; trapping of furbearers; withdrawal of water for consumptiom; removal of riparian forests.
Loading by substances and heat energy	Inert solids and suspensions of sand and clay; nutrient materials that fertilize plants and plankton; poisons and contaminants that harm organisms; heat that raises the temperature of the water.
Restructuring the morphometry of water bodies and flood plains	Damming streams, filling reservoirs with sediments; dyking channels; draining or rebuilding low areas; bulkheading the shoreline; dredging to deepen the channel; stirring up sediments by boating and shipping.
Introduction of non-native organisms	Intentional stocking of preferred organisms which may nevertheless become pests; accidental invansion via canals, ballast water, private aquaria; release or escape from aquaculture facilities or anglers' bait buckets.



	ORDER 1-3	ORDER 4-6	ORDER 7+
RESOURCE HARVESTING		LOGGING MINING ROAD CONSTRUCTION	HYDRO DAMS DIVERSIONS
RURAL, AGRICULTURAL	DITCHING/DRAINING LIVESTOCK IN STREAM CLEARING OF BASIN PONDING	CHANNELIZATION REMOVAL OF WOOD DEBRIS CONSUMPTIVE USE OF WATER RURAL FLOODPLAIN DEVELOPMENT	IRRIGATION DAMS DIVERSIONS TRANSPORT CHANNELS NAVIGATION LOCKS LEVEES, DIKES BANK REVETMENT
URBAN	PAVING OF BASIN CONCRETE STORM CHANNELS BURIAL IN PIPES	CHANNELIZATION BANK ARMOURING DREDGING URBAN FLOODPLAIN DEVELOPMENT	SEQUENTIAL DAMS DOCK FACILITIES BULKHEADS PIERS, SLIPS

FIG. 2. Structural degradation of river systems used by humans. The vertical axis represents mode of land use; the horizontal axis is river size.

Small rivers are linked to the landscape by virtue of their small size, relatively large surface area/volume ratio, and their great abundance relative to larger watercourses. Decoupling and degradation occur primarily through removal of riparian forest vegetation. In extreme form, biotic riparian influence is totally excluded by burying the stream in a pipe. In this transformation complex energy sources and structure (leaves, wood debris, terrestrial insects) and a relatively benign hydrological environment are replaced by harmful inputs (sewage) and disruptive energy inputs (urban storm waters).

Large rivers are linked to the landscape by virtue of extensive floodplains and complex channel patterns. Because of their greater width and relatively short length, riparian effects are relatively unimportant under low flow conditions. Decoupling and degradation occurs through channelization or flow regulation, confining the river to a single channel and denying it annual or more frequent access to its floodplain. Many of the riparian inputs to small streams, as noted above, occur in an analogous way on the floodplain of large rivers. Large rivers go to the forest at times of flood, rather than waiting for forest inputs as is the case with small streams.

Welcome (1985) has summarized how large river ecosystems may be transformed under the mix of interventions typical of conventional exploitative development (Table 4). The third column in Table 4, entitled "Fisheries" show a sequence that leads, through stages, toward a general stress syndrome as sketched in Table 3. Figure 3 (from Welcome 1985) shows what usually happens as fishing intensifies in the context of exploitative development. As depicted here, only the fishing stress is intensifying progressively; this is seldom the case, — usually a variety of other use-stresses are also intensifying and contribute to the syndrome. Most other stresses act to make the fish association more vulnerable to an exploitative fishery. Also they usually act directly to suppress most of the more desirable species through a variety of causal mechanisms. Regier (1979) has sketched some of these causal connections for lake and lit-

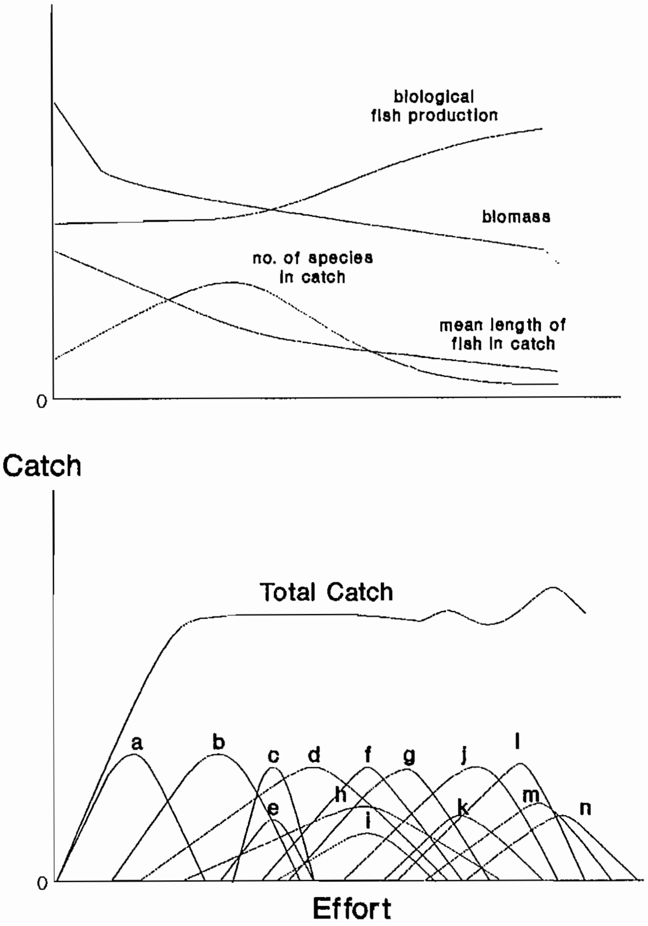


FIG. 3. Theoretical changes in a fish community when subjected to increasing fishing pressure: *(top)* of certain population and fishery parameters; *(bottom)* of total catch and catch of individual species «a» through «n».

TABLE 4. Stages in the modification of rivers.

Stage	Basin use	Fisheries	Research and management problems
Unmodified Channel and floodplain show most characteristic features, flood regime unhindered by direct human interventions, but indirect effects of activities elsewhere in the river basin may be apparent, e.g., Sepik, Niger, Sudd	In wild state often forested, supports game and later used for grazing cattle. Vegetation modified by burning. Seasonal occupation by nomadic fishermen, hunters and pastoralists. Slash and burn agriculture practised in basin.	Fish stocks largely in original condition of diversity but size structure may be modified by fishing in both river channels and standing waters. Whole channel and plain available for fisheries. Accidental introductions could result in the presence of several exotic fish species.	Exploratory fishing for description of composition of fish stock. Identification of major resources. Studies of biology of individual species and their geographical and seasonal distribution. Studies on local fishing methods and introduction of appropriate additional techniques. Establishment of simple regulatory measures for protection of major stocks. Improve access and marketing network.
Slightly modified Some drainage channels for more rapid and efficient removal of flood waters from floodplain. Smaller depressions filled or regularized. Flood still largely unaltered in timing and duration. Some small dams on lower order streams, e.g., Senegal, Oueme.	Floodplain largely cleared of forest, extensive drawdown agriculture, some floating rice in suitable depressions. Some areas reserved for grazing and zonation of floodplain for different uses often highly developed. Settlement on levées and higher ground, or on artificial islands and stilt villages.	Fish stock largely unaltered although larger species may be becoming rarer and size structure heavily biased toward smaller individuals. Some depressions may be dammed as holding ponds, or for extensive aquaculture, or fish holes may be excavated. Whole floodplain available for fisheries.	Population dynamics of major elements of community to give refined estimates of potential yields. Continue studies on biology to identify possible subpopulations and to describe ecological interactions between species. Monitoring of fishery to detect potential over-fishing of major stocks coupled with intensification of regulatory measures to protect fish stock. Investigation of simple forms of extensive aquaculture. Improvement and concentration of fish landings and preservation techniques.
Extensively modified Lower order streams largely dammed for flood control or irrigation. Drainage and irrigation common, some flood control through dams and levées which contain main channel. Depressions usually filled or regularized. Flood often modified in timing and duration, e.g., Chao Phrya, Mekong.	Flood agriculture (usually rice) and intensive dry season agriculture. Moderately extensive occupation of the dryer areas of the plain for habitation — beginnings of urbanization. Much of plain still subject to flooding. Degradation of lower order streams through degradation of environment produced by deforestation and intensive agriculture, mining, industrial pollutants and urban sewage entering river frequently without treatment. Pesticides and herbicides from large-scale monoculture treatment also enter the river.	Some modification to fish stock with disappearance of larger species. Wild fisheries often very intense in main river channels, with some new fisheries in reservoirs. Disappearance of most long-distance migrant species. Rice fish culture in suitable areas. Drain-in ponds and some intensive fish culture in regularized depressions. River area available for fisheries restricted.	Examination of general dynamics of fish community to judge reaction to various sources of loading. Intensification of monitoring of fisheries with increased control of catching methods by licensing and legislation. Examine impacts of other activities in the river basin on the fishery and endeavour to ensure that suitable conditions are maintained. Investigation of intensive aquaculture methods. Consider development of reservoir fisheries and seek alternative employment to reduce fishing pressure on main river.
Completely modified Flood control by large upstream dams and by levées. Main channel sometimes channelized. Flood-plain largely dry although still subject to occasional catastrophic floods. River often reduced to a chain of reservoirs, e.g., Mississippi.	Urbanization, intensive use of river basin for agriculture, industry, habitation. Mining, industrial and urban pollution to some degree controlled, eutrophication usual. Pesticides and herbicides input.	Fish stock changed by loss of some species through pollution and channelization and sometimes by introduction of exotic species. Some sport fisheries in main channels or in few lakes that have been retained on flood-plain. Some intensive aquaculture in specially constructed ponds. River area available for fisheries very small, but intensive fisheries may be developed in the reservoirs.	Investigation of eutrophication and pollution and other management impacts to establish criteria for maintenance of fish stock. Regulation of discharge and effluent according to these criteria. Contemplate introduction of new elements to fish community or stocking to support threatened species. Study access problems to fishery to resolve conflicting demands of sport and commercial fishermen. Intensify development of aquaculture and reservoir fisheries.

toral fish associations; Welcome (1985) has provided a similar analysis for riverine parts of the basin ecosystem.

The fourth column in Table 4 lists the kinds of research and management problems usually addressed during the successive stages of exploitative development. Usually the researchers and managers have responded to challenges as those have emerged: there has been relatively limited foresight on which to base research and management initiatives so as to forestall or meliorate the usual adverse consequences of conventional exploitative development. Understanding may now suffice for preventive as well as corrective action, in addition to the merely reactive responses.

River Rehabilitation

Rehabilitation practice for rivers (Fig. 4) reflects the nature of river degradation as outlined above. Methodologies applied to small rivers are concerned mainly with replacing lost riparian components; methodologies applied to large rivers (there are not yet many examples) are concerned mainly with ameliorating or limiting floodplain isolation and restoring some geomorphic diversity.

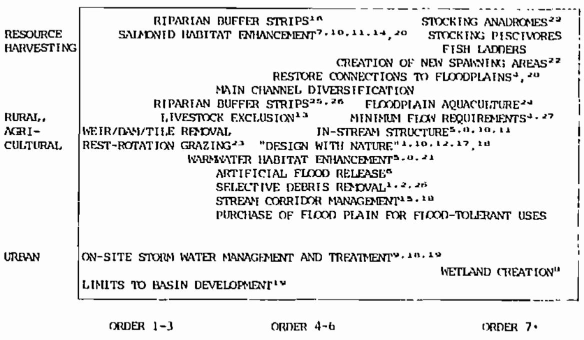
Ecosystem Concepts of Practical Use For Large River Rehabilitation

Ecosystem States: Healthy and Pathological

In a relatively benign setting that provides all the various systemic necessities (with respect to both means and their variances), living systems tend to develop, or evolve along lines that are predictable in general but not in detail. L. von Bertalanffy (see Davidson 1983, p. 86–87) characterized such development as follows:

> ''As life ascends the ladder of complexity, there is progressive integration, in which the parts become more dependent on the whole, and progressive differentiation, in which the parts become more specialized. In consequence, the [living system] exhibits a wider repertoire of behavior. But this is paid for by progressive mechanization, which is the limiting of the parts to a single function, and progressive centralization, in which there emerge leading parts...that dominate the behavior of the system''.

Bertalanffy felt that this set of processes applied not only to organisms but also to other living systems. Steedman and Regier (1987) have applied this self-organizational concept to ecosystems, with which Bertalanffy apparently had little experience. They noted that the ecosystem degradative process (as with conventional exploitative development) runs counter to this ''Bertalanffian succession''.



References

1. AFS (1983); 2. Benke et al. (1985); 3. Binder et al. (1983); 4. Bravard et al. (1986); 5. Carline and Klosiewski (1985); 6. Coke and Pott (1970); 7. DFO (1980); 8. Edwards et al. (1984); 9. Field (1905); 10. Gore (1985) (several papers); 11. House and Boehne (1986); 12. Jordan (1984); 13. Keller and Burnham (1982); 14. King et al. (1980); 15. Marsh and Luey (1982); 16. Murphy et al. (1986); 17. Newbury and Gaboury (1987) 18. Nunnally (1985); 19. NYDEC (1986); 20. OMNR (1984a); 21. OMNR (1984b); 22. Pavlov and Vilenkin (1908); 23. Platts and Nelson (1985); 24. Ravagnon (1978); 25. Schlosser and Karr (1981); 26. Shields (1982); 27. Stalnaker (1981); 28. Welcomme (1985)

FIG. 4. Rehabilitation methodologies for river systems, with selected references to practical application. The vertical axis represents mode of land use; the horizontal axis is river size.

Perturbation ecologists have noted that natural stochastic phenomena act as partial rejuvenation or re-set events that seem, on the whole, to be beneficial for the long-term persistence of the ecosystem. Stresses initiated by exploitative humans generally are different from natural perturbations. Intense stresses of human or cultural origin tend to intrude more deeply into the ecosystem, apply more widely in space, persist longer in time and often involve uniquely new phenomena. Hence undesirable features of stress pathology initiated by humans often go beyond the usual limits of re-set events due to natural perturbations. This new domain of degradation may be termed pathological rejuvenescence or pseudo-rejuvenescence, in contrast to the effects of most natural perturbations which cause natural rejuvenescence in the form of moderate re-sets. Protagonists for a particular stressful development, or apologists for the consequences of such a development, may claim that nothing more than pre-existent natural perturbing phenomena are involved. After all, one can find symptoms triggered by natural perturbations that resemble some of those of degrading human stresses. But there is more to it than that! An ecosystem that has been intensely degraded by humans may spontaneously recover little of its former primeval character following relaxation of some or all of the human stresses, at least within a finite time interval. It may have been crippled, through permanent loss or inactivation of important structures, elements and processes. Hence, the need, usually, for active restoration and/or thorough-going mitigation, to complement remediation in an overall program of rehabilitation.

Stress Ecology

Generally, ecosystems accommodate rather effectively to natural perturbations or disturbances of some magnitude and intensity. Close equilibrium is not to be expected in natural ecosystems; deviations from some abstract equilibrium point are the rule rather than the exception. Not only are all things in states of flux, but they are in states of varying flux. The parameters that may be associated with the variations may be more important than those associated with an equilibrium point, both for purposes of understanding and of management. Technically advanced and economically exploitative humans impose cultural stresses which also have their measures of mean and variance, temporally and spatially.

The influence of an additional human stress on a river in which natural perturbations and human stress regimes are not changing much, has often been assessed prior to a proposed development and has sometimes been monitored after the event. To characterize quantitatively and qualitatively the consequences of just one additional stress, against a relatively fixed background, is a difficult task. If the issue is complicated by the addition of two human stresses, which intensify concurrently and perhaps interact synergistically, any attempt to infer consequences becomes very difficult indeed. By extension it would be practically impossible to assess cumulative impacts of three stresses. Nevertheless concurrent intensification of several stresses has been occurring in recent decades in rivers and other aquatic ecosystems. Are we left without a useful approach to a comprehension of the effects of such complicated intensifying regimes of human stresses?

This puzzle has led to a search for an alternative approach to the usual analysis of population dynamics and flows of energy and materials within and through an ecosystem. One problem was to explain some undesirable phenomena in Western Lake Erie, an estuary-like extension of the Detroit River. Regier et al. (1969) found numerous hypotheses being offered to explain the bad features. On checking these, they found evidence in support of each. They also noted that certain items of evidence were cited by different experts in support of different causes. It became apparent that some of the symptoms were rather generalized and were not uniquely diagnostic of particular stresses. Was it possible that a general stress syndrome might be characterized at an ecosystem level as analogous to the general stress syndrome of Selye (1974) at an organismal level? A variety of human stresses (Table 3), as conventionally practised, appear to generate symptoms some of which appear to be common to most of the stresses (Table 2). These common symptoms together may be termed an ecological general stress syndrome (Rapport et al. 1985). They connot be used simply to diagnose particular causes of the degraded condition.

In the Western Lake Erie situation, 20 years ago, some experts on particular stresses were using non-diagnostic symptoms as evidence that their respective stress (in which each expert had come to have a vested interest) was to blame. Such practice tends to discredit ecological science. Presumably each type of stress also generates some symptoms that are uniquely diagnostic; if known, these may be used to infer at least part of the cause of undesirable effects.

Reconsider the four processes discussed by Bertalanffy: integration, differentiation, mechanization, and centralization. These four self-organizational processes contribute to what Bertalanffy (1950) termed anamorphosis, which occurs in open systems which continuously exchange matter and/or energy with their surroundings. He noted that development in open systems may lead from different starting points and in different ways to the same end-point, and designated this as an equifinality principle. Steedman and Regier (1987) have noted that the occurrence of a general stress syndrome of ecosystem degradation with a common set of symptoms, almost regardless of the kind of intense human stress, may also imply an equifinality principle with respect to such degradation.

One of the practical uses of an ecosystemic general stress syndrome was to warn against unreliable attribution of cause on the basis of ambiguous evidence. It also should lead to a clearer specification of the full set of consequences of a particular stress — which consequences are unique and which are not — but this knowledge has been slow to develop.

Where an ecosystemic general stress syndrome exists, a generic impact assessment for an additional stress can be proposed: the undesirable features of the general stress syndrome will be intensified. There may be exceptions to this general rule (see Steedman and Regier 1987). Intensification of the syndrome with an additional stress loading may sometimes appear disproportionately great. This may be due to synergism in that the new stress may act to intensify the effects of the mix of other stresses in addition to contributing its own immediate effects (Harris et al. 1982; Francis et al. 1985). Conversely, relaxation of a stress that is particularly synergistic may eventually lead to disproportionately large rehabilitative improvements. Harris et al. (1982) used this idea to propose priorities in rehabilitating the Fox River and Southern Green Bay in Wisconsin, USA. But not all cultural stresses contribute always to such a syndrome (Rapport et al. 1985), hence the concept should be applied with caution.

Ecosystem Structure

A Land-River-Bay Continuum — Rivers are aquatic ecosystems interposed between upstream tributaries and drainage areas, and downstream receiving waters such as estuaries, bays, lakes or oceans. The form of an alluvial river reach is primarily determined by the geomorphic regime of upstream components of the river system. The ecology of the same river reach is under strong influence of upstream geomorphology, but is also affected strongly by movements of fish, aquatic birds, mammals, seiches or tides from downstream areas.

A similar point can be made concerning seasonal or periodic lateral expansions and contractions of the width of the river, from the river channel onto flood plains and eventually back into the main channel again. A river may be as much influenced by ecological phenomena on the floodplain as the floodplain is influenced by the state of the river that invades it.

These considerations led to a broadening or extension of the river continuum concept (Vannote et al. 1980; Minshall et al. 1985). Comprehension of degradative and rehabilitative transformations of river ecosystems requires that phenomena beyond the river mouth, and beyond banks of both large and small channels, be incorporated into appropriate conceptual models (Cummins et al. 1984; Francis et al. 1985; Steedman and Regier 1987; Steedman 1988).

Water-Substrate Interfaces — Biotic assemblages that are closely associated with substrates that are not subject to frequent disruption often exhibit great structural organization in aquatic ecosystems. Their relative permanence allows them to develop organization, partially at the "expense" of pelagic associations in the water mass (Margalef 1968). Attached or benthic associations are often well developed in healthy aquatic systems; they are particularly vulnerable to cultural stress of all types, and are often replaced by relatively unorganized associations that bear superficial resemblance to natural pelagic associations.

Dominant organisms — Large aquatic animals, through their longevity, mobility, feeding and behaviour help to integrate ecosystem processes across space and through time. The reproductive processes of such species are often particularly vulnerable to disruption by cultural stresses. Their egg, larval and juvenile stages usually require a recently disturbed environment resembling a pioneer state in the conventional succession paradigm (Regier et al. 1969). Here appropriate food is abundant and predators and competition relatively less intense than elsewhere. In river basins such locales are often on the flood plain or in parts of streams recently disturbed by spates. The adults of these organisms tend to relate closely to the locales in which the ecosystem is developmentally advanced and contains relatively complex habitats such as accumulations of large pieces of wood, rocky rapids, macrophyte beds, or even dunes in sandy rivers.

Centre of Ecological Organization — In trying to comprehend processes of self-organization in ecosystems, it may be more useful to focus initially on information rather than on energy or matter. In ecosystems, two processes that relate strongly to information are the complicated behaviours of reproduction and of predation (Balon 1975). Reproduction involves the transfer of vast information stores in the genome to the next generation. Predation involves the transfer of large amounts of embodied energy (Odum 1986) as food from subdominant to more dominant organisms.

Locales where spawning and rearing take place, and other locales subsequently preferred by adult piscivores and benthivores, we have termed centres of organization (Steedman and Regier 1987). In a general way, we perceive these to be nodes in an information network, and perhaps roughly analogous to ganglia in organisms.

From case studies of ecological degradation due to human stresses, it appears that these two kinds of centres of organization are particularly vulnerable. As the intensity of cultural stress is increased, more and more of these centres are debased and destroyed, decreasing the self-regulatory capabilities of the biotic associations that remain. The biotic association in such degraded systems consists predominantly (in terms of mass, say) of small, short-lived species driven at the mercy of the severely altered hydrologic and physical–chemical regimes. Spatially, there is transformation of biotic associations to a form that bears some resemblance to open lake or other lentic associations. That this does occur is a commonly stated generalization. But the shift from benthic or substrate-associated biota to pelagic forms also involves ''pathological features'', in addition to some of the natural features of the more lentic parts of the system.

Rehabilitation (i.e. including mitigation plus remediation plus restoration) should foster the preservation, reconstitution or recovery of centres of organization. Reconnaissance studies, undertaken in the context of an ecosystem approach, should identify which stresses are mostly responsible for inactivating particular centres of organization. These stresses might then be remediated, i.e. reduced in intensity, and mitigation and restoration be undertaken as appropriate.

Lentic and Lotic Parts of Rivers

On first examination large river environments and the species that occupy them offer a bewildering array of variation and complexity. Rehabilitation strategies based on an individual habitat feature or a particular species are unlikely to prove successul. More general classifications are needed to bring order to this complexity, and coherent distinctions can be made at ecosystem and fish community levels. These distinctions correspond to natural management units in that they tend to respond as a set to exploitational impacts or to management and rehabilitation strategies.

A river during the flood tends to be a moving sheet of water with local differences in depth and flow caused by the morphology of the channel-plain system. At this time, and at the present state of knowledge, it is difficult to make distinctions between classes of habitat. Classifications of riverine features therefore tend to be based more on low-water morphology. A distinction may be made between lotic and lentic components of the system, the former flowing and well oxygenated, the latter stagnant and tending to deoxygenation. The waters concerned are typified on the one hand by the live channels termed ''eupotamon'' by Amoros, Richardot-Coulet and Patou (1982), the other by the ''dead'' waters of scour, slough, oxbow and cutoff lakes lying in the ''plesiopotamon–paleopotamon'' developmental series. A third, intermediate, class of waters can be distinguished, the ''parapotamon'', consisting of backwaters and blind channels that are in contact with the main channel at their downstream ends and thus, while not participating in the active flow at low water, retain communication with the main channel.

The lentic components of river systems in the temperate zone have tended to be suppressed due to human influences on developmental processes since the industrial revolution. These changes are less marked in the arctic and in the tropics where the original relationship between floodplain and channel still persist in many rivers. In the temperate zone some systems still retain sufficient of their original features to indicate that the pristine condition of the waters was not far removed from that pertaining in the tropics today, a supposition further supported by evidence from the historical record.

White, Grey, and Black Fish

In the Mekong River the fish community is traditionnally divided into ''black fish'' and ''white fish'' components. This distinction was extended by Welcomme (1985) to communities from all flood rivers to cover two major behavioural and ecological assemblages of riverine fish. The division is not fully satisfactory as there remains a number of species of intermediate behaviour and we propose to treat these under a third assemblage, ''grey fish'' (which may be multi-coloured).

In general ''white fish'' are associated with the eupotamon, ''black fish'' with the plesiopotamon–paleopotamon series and ''grey fish'' with the parapotamon. Table 5 shows a representative sample of different fish taxa with respect to the various water types. Our classification applies generally at the family or subfamily level with families assigned to white, grey or black fish categories according to the dominant behaviour pattern. Especially large families such as the Cyprinidae or the Mormyridae may have representatives of all types and here typical genera have been indicated.

With respect to the composition of assemblages of different climatic zones, the characteristics of the black fish assemblages become more marked at lower latitudes (Table 6). This may arise for two reasons. Firstly, the oxygen stress characteristics of cold water systems are usually not extreme. The low metabolic rate of all heterothermic organisms at low temperatures has a consequence that oxygen concentrations of the water tend not to be suppressed to low levels between annual or seasonal recharge events. Thus the need for specialized auxiliary air breathing organs is not so high in cold waters. Secondly, most temperate systems are already modified by humans and have lost their inundation

TABLE 5. Some taxa of freshwater fish classified according to their ecological characteristics at various climatic zones.

Climatic zone	White fish	Grey fish	Black fish
Cold Northern	Salmoninae Coregoninae	Catostomidae	Umbridae
North Temperate	Acipenseridae Salmonidae Cyprinidae (Barbus) Clupeidae	Centrarchidae Percidae Cyprinidae (Cyprinus) Esocidae	Umbridae Cyprinidae (Phoxinus) Cobitidae Amiidae
Tropical	Cyprinidae (Probarbus) Characidae Prochilodontidae Mormyridae (Mormyrops) Pimelodidae Pangasiidae	Cyprinidae (Labeo) Distichodontidae Citharinidae Mormyridae (Gnathonemus) Mochokidae Schilbeidae Serrassalmidae Cichlidae	Anabantidae Channidae Erythrinidae Dipnoi Mormyridae (Pollimyrus) Clariidae Notopteridae Gymnarchidae

TABLE 6. Some contrasting features of three ecological assemblages of riverine fish.

Feature	White fish	Grey fish	Black fish
Respiratory organs	Gills	Gills with some physiological adaptations to low dissolved	Gills; supplementary air breathing organs; physiological adaptation to low dissolved oxygen
Respiratory tolerance	Highly oxygenated waters	Medium to low oxygen tensions	Low dissolved oxygen — anoxic
Dominant sense	Eyes	Eyes; electrosensory	Tactile; electrosensory
Muscle fibre type	Red	Red/white	White
Migratory behaviour	Long distance longitudinal	Short distance longitudinal; often long lateral migrations	Local movements mostly
Reproductive guild (after Balon 1975, 1981)	Non-guarders; open substratum spawners; lithophils; pelagophils	Guarders; nest spawners; open substratum spawners, phytophils	Guarders; external and internal bearers; complex nest builders
Body form	Round, streamlined, fusiform	Laterally compressed, spiny, often heavily scaled	Laterally compressed or soft, elongated and flabby; scales reduced or absent
Colour	Silvery or light	Dark, frequently ornamented or coloured	Very dark, often black
Dry season habitat	Main channel (Eupotamon), lake or sea	Backwaters or main channel fringes (Parapotamon)	Floodplain water bodies (Plesiopotamon-paleopotamon)
Wet season habitat	Main channel or flooded plain	Floodplain	Floodplain or marshy fringes

zones. Fish communities have therefore been forced to adjust to these changed conditions with many species being now located in habitats which they did not originally occupy or which were marginal to their range.

White fish species are strongly dependent on the main river for breeding although in many species some aspect of the life cycle may also be associated with the floodplain. There is a strong longitudinal (*sensu* Daget 1960) component to the migratory pattern, usually ascendent for breeding at upstream sites and descendent to feeding areas in lakes or the sea for much of their adult lives.

Black fish species dominate the floodplain. Migrations involve movements out of the confines of the dry season refugia in the permanent water bodies and onto the plain or into marshy areas at the fringes of the flooded area.

Grey fish tend to inhabit backwaters, fringing vegetation, the edges of larger floodplain lakes or the stagnant main channel during the dry season. Longitudinal components of their migrations are generally limited but there is usually a strong lateral component from main channel to floodplain for breeding and feeding during the floods. Species in this group are usually more facultative in their behaviour than either white or black fishes. Behaviourally, they appear to have both migratory and static/territorial components which enable them to adapt more readily to changing hydrological conditions within the aquatic system.

Each association is vulnerable to particular types of modification to the ecosystem. Structures which block the main channel, thereby preventing longitudinal movement within the river channel, tend to affect white fish species. Indeed most species that have been eliminated following the installation of large dams in rivers have been of this type. Structures that enclose or isolate the floodplain suppress the black fish species, although here effects are apt to be more general as young white fish are also dependent on the plain for food. Shore works and channelization might be thought to attack grey fish selectively, but through their greater flexibility these emerge as dominant within modified ecosystems. The term "apparently" is used here advisedly as the precise nature of the components within the grey fish class — be they races, behavioural subspecies or merely a proportion of a population independent of genetic factors — is not yet clear. More generally, cumulative changes in hydrology and morphology of a floodplain river system will progressively affect all components of the community inducing major shifts in species dominance, relative and total abundance and yield.

Biotic Integrity

Recent practical initiatives to assess ecosystem health have attempted to address biotic or ecological integrity directly. In part these have been motivated by political commitments such as that stated in the purpose of the 1978 Great Lakes Water Quality Agreement (IJC 1978).

In practice, "undisturbed" aquatic systems have been defined to have high biotic integrity, and changes in biotic integrity are measured relative to this standard. An undisturbed river system would occur within a watershed vegetated by the mature, natural vegetation of the region, with no major contamination or pollution inputs, and no channel modifications (Hughes 1985). Such systems, where they occur, exhibit heterogeneous channel morphometry, well-developed floodplain features, good water quality and ecologically diverse and abundant fish associations (Hesse 1987; Bravard et al. 1986; Karr et al. 1985; Sedell and Froggatt 1984; Triska 1984).

For a variety of reasons including their size, longevity, habitat requirements and economic value, fish associations are often chosen as indicators of biotic integrity in rivers (Hendricks et al. 1980; Karr 1981; Fausch et al. 1984; Angermeier and Karr 1986; Leonard and Orth 1986; Steedman 1988). Most of these approaches, however, have been developed and applied mainly in small— to medium-sized rivers (i.e. up to 6-7 order). An approach based on integrative measures of health at several levels of ecological organization, all standardized according to regional criteria for "excellent health", should be applicable and valuable for the ecological assessment of larger rivers worldwide. The ecological taxa of white, grey and black fish, for example, are easily incorporated into this methodology, and could provide practical integrative measures of the ecological state of large river systems.

Closing Comments

Human uses of large ecosystems may be manageable, but large aquatic ecosystems themselves are not manageable in any realistic sense of the word. Much effort bas been devoted to managing human uses, ostensibly so that the quality of the water remains swimmable, drinkable, and fishable and the quality and quantity of the resources are maintained in sustainable and enjoyable condition. Overall there is a sixth goal: that the mix of uses be equitable as shared among legitimate users, usually with priority given to sensitive users that depend on a high quality of the aquatic ecosystem.

Heretofore few if any uses of aquatic ecosystems have been managed so as to prevent serious compromise of one or more of the six goals above. In the most highly developed watersheds, all goals are compromised with a result that aquatic ecosystems have been degraded to the obnoxious status of an ecological slum. Part of the reason must rest with the inadequate state of ecosystemic science and technology. Specialists on particular taxa, habitats, techniques, instruments or human uses and abuses have tended to promote their own interest against protagonists for more inclusive interdisciplinary study. Recently there has been some correction of this imbalance.

A self-organizational perspective is increasingly being used by scientists researching "systems" (Rapoport 1986). In a system context there are useful roles for terms such as identity, health and integrity, though these words may irritate reductionists and conventional specialists. Science relevant to the ecosystem approach will increasingly entrain relevant specialists and reductionists, including some that will continue to complain about the approach that they are then serving.

The problem for us is not how to gain acceptance of an ecosystem approach, — that process is already under way. The problem is how to foster further development of a paradigm consistent with an ecosystem approach that is particularly relevant and cost-effective for rehabilitating degraded aquatic ecosystems. That is what this paper is all about, but we do not presume to suggest that what we have presented is sufficient for that purpose.

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References

AFS. 1983. Stream obstruction removal guidelines. American Fisheries Society, Bethesda, MD. 9 p.

AMOROS, C., M. RICHARDOT-COULET, AND G. PATOU. Les 'Ensembles Fonctionelles': des entités écologiques qui traduisent l'évolution de l'hydrosystème en intégrant la géomorphologie et l'anthropisation (exemple du Haut-Rhône français). Rev. Géographie de Lyon 57: 49–62.

Angermeier, P.L., and J.R. Karr. 1986. Applying an index of biotic integrity based on stream fish communities: considerations on sampling and interpretation. North Am. J. Fish. Man. 6: 418–429.

Balon, E.K. 1975. Reproductive guilds of fishes: a proposal and definition. J. Fish. Res. Board Can. 32: 821–864.

1981. Additions and amendments to the classification of reproductive styles in fishes. Environ. Biol. Fish. 6: 377–389.

Benke, A.C., R.L. Henry, III, D.M. Gillespie, and R.J. Hunter. 1985. Importance of snag habitat for animal production in Southeastern streams. Fisheries 10(5): 8–13.

Bertalanffy, L. von. 1950. The theory of open systems in physics and biology. Science 111: 23–29.

Binder, W., P. Jurging, and J. Karl. 1983. Natural river engineering — characteristics and limitations. Garten und Landschaft 2/83: 91–94.

Bravard, J.P., C. Amoros, and G. Patou. 1986. Impact of civil engineering works on the successions of communities in a fluvial system. Oikos 47: 92–111.

Carline, R.F., and S.P. Klosiewski. 1985. Responses of fish populations to mitigation structures in two small channelized streams in Ohio. N. Am. J. Fish. Man. 5: 1–11

Coke, M., and R. Pott. 1970. The Pangalo floodplain pans: a plea for conservation. Pietermaritzberg, Natal Parks Board. 34 p.

Cummins, K.W., G.W. Minshall, J.R. Sedell, C.E. Cushing, and R.C. Petersen. 1984. Stream ecosystem theory. Verh. Internat. Verein. Limnol. 22: 1818–1827.

Daget, J. 1960. Les migration des poissons dans les eaux douces tropicals africaines. Proc. IPFC 8: 79–82.

Davidson, M. 1983. Uncommon sense — the life and thought of Ludwig von Bertalanffy. J.P. Tarcher, Inc., Los Angeles, CA. 247 p.

DFO. 1980. Stream enhancement guide. Government of Canada, Department of Fisheries and Oceans. Vancouver, B.C. 96 p.

Edwards, C.J., B.L. Griswold, R.A. Tubb, E.C. Weber, and L.C. Woods. 1984. Mitigating effects of articifial riffles and pools on the fauna of a channelized stream. N. Am. J. Fish. Man. 4: 194–203.

FAO. 1985. Proceedings of the World Conference on Fisheries Management. Food and Agriculture Organization, Rome Italy.

Fausch, K.D., J.R., Karr, and P.R. Yant. 1984. Regional application of an index of biotic integrity based on stream fish communities. Trans. Am. Fish. Soc. 113: 39–55.

Field, R. 1985. Urban runoff: pollution sources, control, and treatment. Water Res. Bull. 21: 197–206.

Francis, G.R., A.P. Grima, H.A. Regier, and T.H. Whillans 1985. A prospectus for the management of the Long Point ecosystem. Great Lakes Fish. Comm. Tech. Rep. 43: 109 p.

Gore, J.A. [ed.]. 1985. The restoration of streams and rivers. Butterworth Publishers, Boston, MA. 280 p.

Harris, H.J., D.R. Talhelm, J.J. Magnuson, and A.M. Forbes. 1982. Green Bay in the future — a rehabilitative prospectus. Great Lakes Fish. Comm. Tech. Rep. 38: 59.

Hendricks, M.L., C.H. Hocutt, and J.R. Stauffer, Jr. 1980. Monitoring of fish in lotic habitats, p. 205–231. *In* C.H. Hocutt and J.R. Stauffer [ed.] Biological monitoring of fish. Lexington Books, D.C. Heath and Co, Lexington MA. 417 p.

Hesse, L.W. 1987. Taming the wild Missouri River: what has it cost? Fisheries 12(2): 2–9.

Hocutt, C.H. 1981. Fish as indicators of biological integrity. Fisheries 6(6): 28–31.

House, R.A., and P.L. Boehne. 1986. Effects of instream structures on salmonid habitat in Tobe Creek, Oregon. N. Am. J. Fish. Man. 6: 38–46.

Hughes, R.M. 1985. Use of watershed characteristics to select control streams for estimating effects of metal mining wastes on extensively disturbed streams. Environ. Man. 9: 253–262.

IJC. 1978. The Great Lakes Water Quality Agreement of 1978. International Joint Commission, Ottawa, Canada and Washington, U.S.A. 47 p.

Jordon, W.R., III. 1984. Working with the river. Restoration and Management Notes 2(1): 4–11.

Karr, J.R. 1981. Assessment of biotic integrity using fish communities. Fisheries 6(6): 21–27.

Karr, J.R., L.A. Toth, and D.R. Dudley. 1985. Fish communities of Midwestern rivers. Bioscience 35: 90–95.

Keller, C.R., and K.P. Burnham. 1982. Riparian fencing, grazing, and trout habitat preference on Summitt Creek, Idaho. N. Am. J. Fish. Man. 2: 53–59.

King, W., F. Richardson, J. Peters, and M. Riedel. 1980. Wild Trout II, Proceedings. Trout Unlimited and Federation of Fly Fisherman. 164 p.

Leonard, P.M., and D.J. Orth. 1986. Application and testing of an index of biotic integrity in small, coolwater streams. Trans. Am. Fish. Soc. 115: 401–414.

Margalef, R. 1968. Perspectives in ecological theory. Univ. Chicago Press, Chicago, IL., 111 p.

Marsh, P.C., and J.E. Luey. 1982. Cases for aquatic life within agricultural watersheds. Fisheries 7(6): 16–19, 24.

Meisner, J.D., J.L. Goodier, H.A. Regier, B.J. Shuter and W.J. Christie. 1987. An assessment of the effects of climate warming on Great Lakes Basin fishes. J. Great Lakes Res. 13: 340–352.

Minshall, G.W., K.W. Cummins, R.C. Peterson, C.E. Cushing, D.A. Bruns, J.R. Sedell, and R.J. Vannote. 1985. Developments in stream ecosystem theory. Can. J. Fish. Aquat. Sci. 42: 1045–1055.

Murphy, M.L., J. Heifetz, S.W. Johnson, K.V. Koski, and J.F. Thedinga. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. Can. J. Fish. Aquat. Sci. 43: 1521–1533.

Newbury, R.W., and M. Gaboury. 1987. Use of natural stream characteristics for stream rehabilitation work. Proc. Canadian Water Resources Ann. Conf., Winnipeg, Man. 22 p.

Nunnally, N.R. 1985. Application of fluvial relationships to planning and design of channel modifications. Environ. Man. 9: 417–426.

NYDEC. 1986. Stream corridor management. New York State Department of Environmental Conservation, Division of Water Quality. Albany, NY. 111 p.

Odum, H.T. 1986. Energy in ecosystems, p. 337–369. *In* N. Polunin [ed.] Ecosystem Theory and Application. NewYork, John Wiley and Sons, Environmental Monographs and Symposia.

OMNR. 1984a. A commnity fisheries involvement program, field manual. Part 1: trout stream rehabilitation manual. Ontario Ministry of Natural Resources, Toronto, Ont. 273 p.

1984b. Proceedings of non-salmonid rehabilitation workshop. Kempenfelt Conference Centre, Barrie, Ontario. Oct. 1–3, 1984. Ontario Ministry on Natural Resources, Toronto, Ont. 417 p.

Pavlov, D.S., and B. Ya Vilenkin 1989. Present state of the environment, biota and fisheries of the Volga River, p. 504-514. *In* D.P. Dodge [ed]. Proceedings of the International Larger River Symposium. Can. Spec. Pub. Fish. Aquat. Sci. 106.

Platts, W.S., and R.L. Nelson. 1985. Impacts of rest-rotation grazing on stream banks in forested watersheds in Idaho. N. Am. J. Fish. Man. 5: 547–556.

Rapoport, A. 1986. General system theory. Abacus Press, Cambridge, MA. 270 p.

Rapport, D.J., H.A. Regier, and T.C. Hutchinson. 1985. Ecosystem behavior under stress. Am. Nat. 125: 617–640.

Ravagnon, G. 1978. Vallicola moderna. Bologna, Edagricole. 283 p.

Regier, H.A. 1979. Changes in species composition of Great Lakes fish communities caused by man. Trans. 44th North American Wildlife and Natural Resources Conference. p. 558–566.

Regier, H.A., A.P. Grima, and T.H. Whillans. 1980. Rehabilitation of the Long Point ecosystem. Univ. Waterloo J. Urban and Environ. Affairs, Contact 12(3): 125–149.

Regier, H.A., V.C. Applegate, and R.A. Ryder. 1969. Ecology and management of the walleye in western Lake Erie. Great Lakes Fish. Comm. Tech. Rep. 15: vii + 101 p.

Schlosser, I.J., and J.R. Karr. 1981. Water quality in agricultural watersheds: impact of riparian vegetation during base flow. Water Res. Bull. 17: 223–240.

Sedell, J.R., and J.L. Froggatt. 1984. Importance of streamside forest to large rivers: the isolation of the Willamette River, Oregon, U.S.A. from its floodplain by snagging and streamside forest removal. Verh. Internat. Verein. Limnol. 22: 1828–1834.

Selye, H. 1974. Stress without distress. The New American Library of Canada Ltd, Scarborough, Ont. 193 p.

Shields, F.D., Jr. 1982. Environmental features for flood control channels. Water. Res. Bull. 18: 779–784.

Stalnaker, C.B. 1981. Low flow as a limiting factor in warmwater streams. American Fisheries Society Warmwater Streams Symposium. Bethesda MD. p. 192–199.

Steedman, R.J. 1988. Modification and assessment of an index of biotic integrity to quantify stream quality in southern Ontario. Can. J. Fish. Aquat. Sci. 45: 492–501.

Steedman, R.J., and H.A. Regier. 1987. Ecosystem science for the Great Lakes: perspectives on degradative and rehabilitative transformations. Can. J. Fish. Aquat. Sci. 44 (Suppl. 2): 95–103.

Triska, F.J. 1984. Role of wood debris in modifying channel geomorphology and riparian areas of a large lowland river under pristine conditions: a historical case study. Verh. Internat. Verein. Limnol. 22: 1876–1892.

Vannote, R.L. G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

Welcomme, R.L. 1985. River fisheries. Food and Agriculture Organization of the United Nations, Rome. FAO Fisheries Technical Report 262, ix + 330 p.

An Overview of the Use of Remote Sensing for the Study of Rivers and River Systems

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Abstract

ELLIS, T. J., AND W. A. WOITOWICH. 1989. An overview of the use of remote sensing for the study of rivers and river systems, p. 98–109. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

This paper provides an introduction to airborne and spaceborne remote sensing, and an overview of studies, conducted for the most part since the early 1970's, which demonstrate the application of remote sensing to hydrological investigations and mapping. Regional applications have included hydrologic modelling, surface water inventory, the mapping of snow cover and floods and land use surveys. At the intermediate scale, remote sensing has been used in floodplain mapping and the study of dam sites and reservoirs. Site-specific assessments of water quality, riverbank conditions and fish habitat have also been conducted.

Remote sensing techniques offer data in ranges of the electromagnetic spectrum other than the visible, and provide a permanent record for verification and historical reference. Except in cases where the level of detail required can only be obtained by on-site observation, remote sensing is generally more cost-effective than intensive programs of field survey and sampling.

Résumé

ELLIS, T. J., AND W. A. WOITOWICH. 1989. An overview of the use of remote sensing for the study of rivers and river systems, p. 98–109. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

La présente étude se veut une introduction à la télédétection aérienne et spatiale et une vue d'ensemble des études effectuées en grande partie depuis le début des années 1970 qui montrent l'application de la télédétection aux études et à la cartographie hydrologiques. À l'échelle régionale, la télédétection sert à la modélisation hydrologique, à l'inventaire des eaux de surface, à la cartographie de la couverture de neige et d'inondations ainsi qu'à des relevés de l'utilisation des terres. À l'échelle intermédiaire, la télédétection a été utilisée pour la cartographie des plaines inondables et l'étude de barrages et de réservoirs. On a aussi effectué des évaluations particulières à des sites pour ce qui est de la qualité de l'eau, de l'état des rives et des habitats du poisson.

Les techniques de télédétection permettent de recueillir des données se situant dans les écarts du spectre électromagnétique autre que le visible et fournissent un archivage permanent qui permet la vérification de données et sert de référence historique. Sauf dans les cas où le niveau de détails nécessaire ne peut être obtenu que par des observations *in situ*, la télédétection est généralement plus rentable que des programmes intensifs de levés et d'échantillonnage sur le terrain.

Introduction

In the past, the study of rivers and river systems has depended on a dense network of point-source measurements and on-site observations. The heavier demand placed on water resources by industrial development and a growing population has increased the need to assess and monitor river systems. A rapid and economical method is, therefore, needed for studying rivers — a method which provides a broader perspective than on-site survey can normally provide.

As remote sensing can furnish synoptic coverage over relatively large areas, hydrologists and water resource managers are evaluating the potential of these data for expanding their data bases in a timely and cost-effective manner.

Background on Remote Sensing Technology

Remote sensing is, literally, the perception of objects from a distant vantage point. Remote sensing is based on the fact that patterns of energy (such as ultraviolet light, visible and infrared light, heat and other forms of electromagnetic energy) coming from features on the earth's surface reveal some of the characteristics of these features (Ontario Centre for Remote Sensing 1979).

Remote sensing involves the recording of the patterns of energy emanating from the earth's surface through the use of sensors carried in aircraft or spacecraft. These sensors can be photographic cameras, video cameras or electronic scanners. The recordings made by the sensors may take the form of pictures, known as "imagery", or numerical data stored on tapes.

As a technique for gathering information, remote sensing has a number of advantages over more traditional field data collection methods. The primary advantage is that a permanent recorded image is acquired of an area. This permanent record can be studied by an interpreter in an office or laboratory at any time. Analysis of the data can be aided by the use of optical, mechanical or electronic devices not available to the scientist in the field, whose analysis of an area must be done from tally sheets and other records of visual information made on-site. The availability of permanent recorded images and the ability to obtain repetitive area coverage with the same parameters allows for the monitoring of an area over time.

Another advantage of remote sensing is that sensors can collect data from ranges of the electromagnetic spectrum not visible to the human eye. There are many conditions in the environment which can only be detected in the non-visual ranges. A decrease in vegetation vigour, for example, can be detected from reduced infrared reflectance before it has manifested itself in visible colour changes.

The fact that remote sensing images are acquired from the vertical perspective, for the most part, produces a synoptic view of an area. The use of remote sensing techniques can thus reduce the need for intensive field surveys over large regions, while increasing the effectiveness of field checking.

The limitations inherent in remote sensing are present in each sensor system to a different degree. They include limitations on the timing of coverage (imposed by the fixed cycle of a satellite, for example, or by daily or seasonal weather fluctuations); limitations on image resolution (as a result of altitude or the fixed "acuity" of the sensor system); and problems with data availability (resulting, for example, from satellite data recording or transmission failures or image production backlogs). The cost of using remote sensing is determined by the size of the coverage area, the level of detail required and the choice of sensor.

The first step in understanding the uses of remote sensing, therefore, is to understand the major sensor systems.

Sensor Systems

For a description of remote sensors and their capabilities, the reader is referred to the Manual of Remote Sensing (Colwell 1983), Remote Sensing Principles and Interpretation (Sabins 1987), the Handbook of Remote Sensing in Fish and Wildlife Management (Best 1982) and other publications listed in the "References" of this paper. The following section provides only a brief outline of some of the available airborne and spaceborne sensors.

Airborne Sensors

Black and white panchromatic airphotos remain the most common form of remote sensing data available. They are usually recorded with enough overlap between frames to permit stereoscopic viewing, a technique which produces a three-dimensional model of the terrain. Normally the low cost of black and white photography makes it feasible to compile archives of periodic coverage. In Canada, the National Air Photo Library maintains an archive of airphoto coverage from across the country. In addition, extensive archives are generally maintained at the provincial level by remote sensing centres, public utilities, resource management agencies and transportation and planning organizations.

In addition to standard black and white films, colour film, colour infrared film and, to a lesser extent, black and white infrared film are also commonly used. The main advantage of colour photography over black and white panchromatic photography is that the interpreter can distinguish a greater number of colour hues than of grey tones. Colour film is essential when the feature of interest can only be detected by its colour, for example, pollution outfall from an industrial site. Colour film also has the ability to "penetrate" clear water; therefore, it is valuable for detecting and delineating underwater features such as shoals and channel obstructions.

Just beyond the visible portion of the electromagnetic spectrum lies the near-infrared range which can be recorded photographically using infrared-sensitive film. This film produces a "false-colour" image of the reflected infrared energy which is otherwise invisible to the human eye. The principal advantages of colour infrared photography are twofold. First, it allows the interpreter to evaluate stress conditions in vegetation before they can be detected from visible light. Secondly, it enhances wet areas and waterbodies, as water absorbs infrared wavelengths and thus appears dark blue or black on the photography.

The technique of recording separate aerial photographs in more than one spectral band at a time over the same target is known as multispectral photography. Multispectral photography can be acquired using special cameras with more than one lens — that is, using black and white film with different lens filters on the same camera — or by operating two or more cameras at the same time, each loaded with a different film. Multispectral photographic coverage offers the possibility of identifying features whose characteristic spectral "signatures" lie beyond the limits of the principal film used. For example, two vegetation types which are difficult to distinguish from each other on a panchromatic photograph may be separable on a black and white infrared photograph.

Video systems are proving to be versatile airborne sensors, and are conveniently portable as well. Although airborne video recording produces low-resolution imagery and can only be used in cloud-free weather, it is of considerable value in acquiring real-time data for monitoring purposes or for non-precision mapping. The principal advantages of video recording are the relatively low cost, the real-time viewing capability and the fact that the users themselves can operate the systems from light aircraft. Both colour and black and white video cameras have been used in recording imagery for hydrological applications (Overton and Mussakowski 1983; Ontario Centre for Remote Sensing 1983).

Aerial thermography is another remote sensing technique which has proven very effective in water resource applications. All objects on the earth's surface radiate thermal infrared energy (heat). Ice and snow radiate less energy than a soil surface in summer, but even the amount of energy coming from a frozen waterbody can be detected, measured and recorded through the electronics of thermal imaging systems.

A thermal line scanner converts radiated heat energy emitted from the earth's surface into electronic signals. These signals are recorded on magnetic tape and played back on a television-like monitor. Prints for use in interpretation are produced by electronically exposing photographic film to the magnetic tape information. These prints, called thermographs, look somewhat like familiar black and white aerial photographs. On the thermographs, however, the light and dark tones represent relative levels of warmth. On positive prints of the imagery, relatively warm areas appear in light shades of grey, while colder areas are darker.

Thermography captures only the heat energy emitted by a feature, and does not depend on visible light. It can, therefore, be recorded at night and in weather conditions unsuitable for aerial photography. In fact, thermography missions are timed for the period when the object of study is in maximum temperature contrast to its surroundings. The temperature contrast may consist of a ''hot'' subject against a cold background or a ''cold'' subject against a warm background. Thermography has been used to study water temperature variations in rivers and streams for fisheries management purposes (Lawrence et al. 1980).

The non-visible-range sensors also include radar sensors, which have the unique ability to penetrate cloud cover. They consist of a transmitter which sends radar signals down to the earth's surface and a receiver which detects the returning waves as they bounce off objects. Smooth surfaces bounce the signal away from the receiver, while rough surfaces deflect the signal so it may be recorded by the sensor. After the flight, the energy returns recorded are processed into visual imagery, which represents various concentrations of signal return by different shades of grey. Oceanographers have used radar imagery to study sea surface state, ice movement and oil spills (Colwell 1983).

Spaceborne Sensors

The principal satellite program specifically designed for the mapping of earth resources has been the NASA-sponsored LANDSAT program. This program began with the launch of LANDSAT 1 (formerly designated the Earth Resources Technology Satellite, or ERTS) into sun-synchronous orbit on July 23, 1972. Since that time, NASA has launched a total of five LANDSAT satellites. The orbit of the satellite was designed to provide repetitive coverage of the same area every 16 to 18 days. Along each of the orbital tracks, LANDSAT's scanners collect data across a 185-km swath. The data are digitally stored on board the spacecraft, then transmitted to a global network of ground receiving stations. From there a range of image products, including computer compatible tapes and hard-copy images in black and white and colour, are distributed in response to orders from users. In Canada, the imagery is received and processed at a satellite receiving station in Prince Albert, Saskatchewan, by the federal government's Canada Centre for Remote Sensing.

The primary sensor on board the first three LANDSAT satellites was the multispectral scanner (MSS), which operated in two visible and two infrared channels, with a spatial resolution of approximately 79 m^2.

The latest satellites in the series, LANDSATs 4 and 5, launched in 1982 and 1985, respectively, each carry two imaging sensors: a multispectral scanner, and an instrument known as the thematic mapper (TM). TM has more advanced radiometric characteristics and spatial resolution than the MSS. TM records a total of six visible and near-infrared channels, with a spatial resolution of approximately 30 m^2, and also a thermal infrared channel with a resolution of 120 m^2.

European countries and Japan have also developed and launched resource satellites. The SPOT satellite was launched by a French corporation of the same name in February, 1986. It produces imagery with the highest resolution which can yet be obtained from a civilian spaceborne platform, surpassing even LANDSAT TM. The satellite's sensors record data with a resolution of 20 m^2 in two visible-light channels and one near-infrared channel, as well as panchromatic data with a resolution of 10 m^2.

Numerous other satellites have been launched during the past 25 years. Meteorological satellites, such as those of the NOAA series, were designed primarily for weather forecasting, but also carry sensors which permit the monitoring of ice conditions in the Arctic. The Coastal Zone Colour Scanner (CZCS) was a satellite sensor designed for the quantitative determination of chlorophyll and sediment in oceans and for measuring sea surface temperature. The spatial resolution was 825 m^2, so images of very large ocean regions were produced, but at a very small scale.

The past decade has also seen development toward specialized airborne and spaceborne sensors such as the sensor for the proposed Canadian RADARSAT satellite and other radar systems, high-resolution scanners such as MEIS (multi-detector electro-optical imaging scanner), and sensors developed specifically for water-resource applications, such as fluorosensors and the laser bathymeter.

An important element in the application of any of these sensors is the verification of the observations with appropriate ''ground truthing''. Ground truthing is field observation and data collection performed to assess the accuracy and precision of the remote sensing data. This field activity may include, for example, the location of coordinates for mapping and the monitoring of turbidity for water resource studies.

The decision as to which sensor is best for an individual resource study can only be made by identifying the strengths of each remote sensing data type, with the understanding that a combination of data types may be needed to produce the most appropriate information.

Applications of Remote Sensing to Rivers and River Systems

All remote sensing coverage can be more or less arbitrarily divided into three categories by scale and scope: small-scale data (from about 1:500 000 to about 1:1 000 000, most useful for regional surveys), medium-scale data (from about 1:15 000 to about 1:60 000, most useful for intermediate-range surveys) and large-scale data (from about 1:1 000 to about 1:20 000, most useful for site-specific investigations).

Small-scale remote sensing data provide multispectral and textural information over large areas at a relatively high level of generalization. Major land cover categories which influence watershed runoff and soil moisture storage can be identified on these data, and the area coverage of each category calculated. The regional perspective of small-scale imagery provides information on the distribution of features and aids in the orientation of features of interest.

Large-scale remote sensing data permit the study and monitoring of some of the factors contributing to water quality at specific sites. For example, the interpreter can observe on a large-scale colour aerial photograph that the discharge into a river of effluent from a factory has a different colour than the river water. Such an observation helps in planning where water samples should be taken.

Remote sensing coverage which falls between the regional and the site-specific provides the primary resource data base for a variety of monitoring and management activities.

The following section reviews remote sensing technologies and data sources for their usefulness in managing water resources and understanding water resource problems.

Regional Surveys using Small-Scale Remote Sensing Data

Today's aircraft and satellite remote sensing systems can contribute to watershed or river basin management in the areas of watershed modelling, surface water inventory, snow mapping, flood management and hydrological land use monitoring. Resource inventory, assessment and monitoring at this scale demands data acquisition techniques which provide repetitive synoptic coverage. Such techniques are based on sensors with large fields of view, such as large-format aerial cameras, multispectral scanners, infrared scanners and radar sensors, operated from high-altitude aircraft and spacecraft. Rango (1975) identified six major areas in which small-scale remote sensing could be applied to hydrology: hydrologic modelling, the inventory of waterbodies, snow mapping, flood mapping, land cover/land use mapping and the study of the physiography of watersheds.

Hydrologic Models

One of the main concerns in hydrology is to develop methods for describing and forecasting the hydrological regime of rivers and watersheds. The information thus obtained provides the basis for hydraulic engineering projects in hydroelectric power generation, water supply and flood control. Martinec (1980) determined that remote sensing is an accurate and efficient source of data on variables which make up hydrologic models, such as surface temperature, soil moisture, sheet flow and other runoff conditions and, in particular, the extent of snow cover. Ragan and Salomonson (1978) reviewed the use of LANDSAT data for defining the input parameters for a variety of hydrologic models. These models were used to synthesize streamflow and water quality parameters in the planning or management processes.

Inventory of Waterbodies

Major decisions on the use and management of inland aquatic resources depend on accurate and detailed mapping of lakes, rivers and streams. In many countries, however, the maps of these inland waterbodies are inaccurate and incomplete. They are particularly deficient in areas that may be important to fisheries but otherwise of low economic value, areas such as river deltas and shallow marsh or swamp lands (Cheney and Rabanal 1984).

The repetitive coverage from the LANDSAT satellite provides a convenient, accurate and inexpensive means of mapping seasonal changes in the surface water area of river systems over large remote regions. Since water absorbs infrared radiation, the non-thermal infrared bands of the LANDSAT multispectral scanner clearly distinguish waterbodies from land masses, and deep, clear water from shallow, turbid water. Areas can be identified which warrant closer investigation with infrared aerial photography or infrared scanners.

Results from numerous LANDSAT-based studies indicate that waterbodies as small as one hectare can be delineated with ease using MSS data. TM data can delineate even smaller waterbodies. The U.S. Army Corps of Engineers has employed LANDSAT MSS data for locating and counting bodies of water larger than 0.02 km^2, calculating their area and identifying their shape, and for locating dam sites on major rivers (Rango 1975). The synoptic view of LANDSAT also shows the geographic relationship of the waterbodies to urban and agricultural areas which may require water supplies. LANDSAT-based techniques for surface water delineation have been used in a U.S. national inventory of lakes and reservoirs larger than four hectares (Rango and O'Neill 1982), and in a reconnaissance survey of natural resources in Namibia. Similar mapping of waterbodies was undertaken in Nigeria using side-looking airborne radar (SLAR) imagery, as part of an assessment of radar imagery for land resource surveys (Cheney and Rabanal 1984).

Since water volume is of great interest to water management personnel, numerous studies have been conducted on remote sensing methods for estimating volume. In Canada, the laser bathymeter has been used with great success for measuring water depths in shallow coastal areas, lakes and rivers (Harper 1983). Radar sensing has also proven effective for measuring the thickness of ice. Thermal infrared measurements often provide an indication of relative depth, as water volume is one of the factors which determine the rate at which a waterbody cools.

In addition to identifying surface waterbodies, satellite data can provide information on geological structures which indicate the location of underground streams. Deductions made from satellite imagery have in many cases formed the basis for successful drilling for water (Harper 1983).

Aerial thermography has also proven to be an excellent method for mapping groundwater discharges of all kinds. When water is warmer or colder than the surrounding land, the contrast can be detected on aerial thermography. The Ontario Centre for Remote Sensing (OCRS) has successfully mapped discharge areas on aerial thermography of the Nine Mile River watershed in Southern Ontario (Lawrence et al. 1980).

In certain areas of the world, scarce water supplies and water-rights laws make it necessary for both the total demand and the demand for irrigation to be calculated. Because of the vast areas involved, remote sensing is used as an aid to planning and decision-making. Remote sensing can determine crop cover types and thus provide information on the need for irrigation, so that statistical estimates of the water demand can be made (Salomonson 1983). Studies using LANDSAT data for this purpose have been conducted in the states of California (Estes et al. 1975), Oregon (Draeger 1977) and Idaho (Heller and Johnson 1979), as well as western Canada (Mollard and Carr 1973) and India (Thiruvengadachari 1981).

Snow Mapping

A great deal of the fresh water of North America comes from melting snow and ice. As a first step in the estimation of snow melt, LANDSAT imagery can provide information on the extent of snow-cover in the winter and the rate of melting in the spring. The area covered by snow can be determined within a few percent, while snow-line altitudes can be determined within 60 m (Harper 1983).

A snow-mapping program completed by NASA has demonstrated that the use of snow-cover data derived from satellite imagery has the potential to reduce the error in estimating runoff from snow-melt. In this study, LANDSAT images were used in determining snowpack extent in three selected river basins in California over a three-year period. The information extracted from the images was shown to have reduced errors in seasonal streamflow forecasting by 10–15%. Modelling studies on the Boise River in Idaho also demonstrated that the use of NOAA weather satellite data could reduce the error in short-term (5-day) forecasts by up to 96%. Through a projection of these results across eleven western U.S. states, it has been estimated that improvements in streamflow prediction from remote sensing data could produce annual benefits in the millions of dollars for hydro power and irrigation (Rango and O'Neill 1982).

Images recorded by the Geostationary Operational Environmental Satellite (GOES) are also being used to monitor river basin snow cover for selected watersheds throughout the western United States and Canada (Yates et al. 1986).

Flood Monitoring and Flood Damage Mapping

Observations of the build-up of snow in the winter and the rate of melting in the spring can provide the basis for flood warnings. LANDSAT imagery is the most pertinent satellite data for flood observation, as inundated areas can be readily detected on the near-infrared bands. The areas affected can be recognized from a reduction in infrared reflectance resulting from standing water, excessive soil moisture, or moisture-stress in the vegetation. In fact, on LANDSAT images recorded as late as two weeks after the flood crest, areas from which the flood water has receded still show a lower level of near-infrared reflectance; therefore, it is not essential for the peak of flooding to coincide with a satellite pass for the imagery to be useful in flood mapping. Flood damage in the United States often exceeds $1 billion annually; thus, any improvement in the process of identifying flood hazard areas and assessing flood damage could produce significant economic benefits. (Yates et al. 1986).

A number of investigators have reported the use of LANDSAT data to map floods (Hallberg et al. 1973; Morrison and Cooley 1973; and Rango and Salomonson 1973). In 1973, an extensive analysis of LANDSAT images for the delineation of the extent of flooding in the entire Mississippi River Valley was carried out by the U.S. Geological Survey (Deutsch and Ruggles 1974). LANDSAT images have been used for assessing flood damage in the states of South Dakota, Iowa and Arizona, and also in Pakistan (Sabins 1978). In the early 1980's, Robinove reported on the role of remote sensing and satellite monitoring systems in hydrologic hazard management, and outlined the interpretation criteria for using LANDSAT imagery for flood mapping, identifying limitations of the method.

Research studies of the 1973 Mississippi River floods, the 1978 Kentucky River floods and the 1978 floods in North and South Dakota indicated that flooded areas showed up well on night-time thermal infrared satellite imagery, as a result of the contrast in temperature between land and water (Yates et al. 1986). Data from satellites of the U.S. National Environmental Satellite, Data and Information Service (NESDIS) has been used for the operational monitoring of floods in support of National Weather Service river forecast centres (Yates et al. 1986).

In April, 1975, LANDSAT images were used to delineate flooded areas in Louisiana. The flood boundaries were then compared with land-use classification maps to determine the extent of flood damage to urban areas, farmland and other cover types. The resulting data were used by the state government for analyzing damage and documenting the need for federal disaster-relief funds (Sabins 1978).

Land Cover/Land Use Mapping

Land cover/land use information produced by the classification of LANDSAT data can indicate the degree of imperviousness of the surface, a factor influencing water runoff. In a 1985 study, land cover/land use information derived from LANDSAT classification results was used in conjunction with the Soil Conservation Service curve-number method to estimate a basin-wide runoff index (Still and Shih 1985).

NASA and the U.S. Army Corps of Engineers tested the operational usefulness of LANDSAT data in obtaining land use information for flood-frequency studies. Using LANDSAT-derived land use data for five test river basins, researchers generated discharge-frequency curves almost identical to those produced by the conventional technique. The average misclassification of the major land use categories was only 2% to 8%. The data also proved easy to handle, and costs were one-quarter to one-half those of conventional techniques, over river basins greater than 25 km^2. A further advantage of LANDSAT-derived land use/land cover classification is that data can be stored directly on a grid-cell basis. An automated environment can thus be created for applying LANDSAT classifications to routine hydrologic investigations (Rango and O'Neill 1982).

In 1985, Ontario Hydro commissioned a land use/land cover survey of the Little Jackfish River basin of north-central Ontario, based on the digital analysis of LANDSAT data. The conclusion from this survey was that, for extensive study areas where access costs are high, remote sensing can provide timely and cost-effective information for use in the environmental planning and assessment of potential hydroelectric developments (Sears 1985).

A U.S. national study employed LANDSAT data to assess and predict water quality in rivers and lakes from existing patterns of land use. For a region consisting of 225 drainage areas, the LANDSAT-based land use mapping produced significant savings in time and money over conventional mapping techniques (Rogers et al. 1975).

In 1984, both conventional aerial photography and satellite imagery were used in determining whether the improper management of agricultural land was contributing to the decline of a commercial fishery in southwestern Manitoba. The digital analysis of LANDSAT data provided a cost-effective, rapid and accurate summary of land use at specific times (Pokrant and Hildebrand 1984).

Jensen et al. (1986) used various remote sensors to map a range of wetland conditions along the Savannah River in South Carolina. LANDSAT MSS data were used for both the regional and detailed mapping of the wetland vegetation cover. Aerial thermography proved valuable in relating vegetation types to surface water conditions, and also provided information on the temperature and spatial distribution of thermal effluents entering the wetlands. Multi-data aerial photography was used to document changes in the wetlands.

Physiographic Characteristics

Data on such physiographic features as the area and shape of river basins, the organization of stream networks and the nature and density of the drainage pattern permit an investigator to estimate the mean annual discharge and flood flow from a watershed. The rapidity of watershed response to a particular rainfall event can also be estimated. Although topographic maps provide important information on physiography as it relates to the study of rivers, the repetitive recording of satellite imagery permits the study of dynamic events. A study in a variety of U.S. physiographic regions found that LANDSAT provided assessments of watershed area, watershed shape and channel sinuosity which were comparable to assessments derived from topographic maps. On 1:100 000-scale LANDSAT enlargements, drainage networks were successfully delineated in areas of dissected relief, although low-order streams were difficult to detect in heavily vegetated areas with little local relief or in areas where stream channel development was limited. The availability of different seasons of LANDSAT imagery slightly improved the detection of physiographic detail in these areas; however, only the use of high-altitude photography provided a marked improvement in feature discrimination. The combination of LANDSAT imagery and aerial photography permitted the extraction of all physiographic parameters necessary for a watershed analysis, with the exception of detailed channel dimensions (Rango 1975).

Intermediate-Range Studies using Medium-Scale Remote Sensing Data

Airborne and spaceborne remote sensing systems have numerous applications to intermediate-range river studies (somewhere between regional surveys and detailed site-specific studies), primarily in the areas of floodplain mapping, water quality monitoring, dam site and reservoir monitoring and habitat analysis. Below the regional scale of study, the assessment and monitoring of rivers may require a combination of remote sensing data acquisition and ground data collection and analysis.

Floodplain Mapping

Floodplain mapping includes the classification of land cover and the analysis of drainage. Colour and colour infrared aerial photography and satellite imagery and digital data are useful for this application area.

Rango and Anderson (1974) successfully delineated the boundaries of a floodplain on the Mississippi River using 1:100 000-scale LANDSAT images recorded prior to flooding. In a related study over a watershed in Pennsylvania, Sollers et al. (1978) found that, because of the large number of aerial photographs required to cover the study site, it was easier to use LANDSAT data to delineate the floodplain on the basis of soil conditions. Singhroy and Wightman (1981) used stereoscopic airphoto interpretation and digital analysis of LANDSAT MSS data for floodplain mapping and land cover classification of the Annapolis River in Nova Scotia. The interpretation of colour infrared photography proved particularly useful for floodplain mapping. Parry and Turner (1971) also found infrared photography a superior data source for drainage analysis and channel detection in small drainage basins.

On floodplains such as the Sudd in Sudan and the Central Delta of the Niger in Mali, the fishery depends heavily on the extent of flooding and the type and distribution of vegetation in the plain. In the late 1970's, the United Nations Food and Agriculture Organization examined the uses of remote sensing in studying inland fisheries, and determined that LANDSAT imagery was valuable in defining flood limits, as well as for identifying residual pools in the dry season and monitoring changes in vegetation cover from one season to the next. The study concluded, however, that LANDSAT's most important role was to provide a source of information for planning sampling programs and stratifying a floodplain according to its probable use for fisheries (Howard and Welcomme 1977). The same study noted that aerial photographic surveys had proven useful in defining the area of a river in West Africa which was used for fish ponds. In 1981, LANDSAT data were used to estimate the minimum and maximum inundated areas of the Amazon floodplain in Peru, for fishery evaluation purposes (Cheney and Rabanal 1984).

Water Quality Monitoring

Pollutants, suspended sediments and aquatic vegetation can be detected on photographic and non-photographic imagery recorded from aircraft and spacecraft.

Pollutants can be detected by their colour on normal colour film and colour infrared film. In 1968, the Water Resources Commission of Massachusetts conducted a demonstration project with Itek Corporation to obtain colour and colour infrared photography of Boston Harbour and evaluate its utility for detecting sources of pollution, analyzing the dispersion pattern of effluent from known sources and assessing water quality. Results indicated that normal colour photography was more useful for detecting large outfalls and colour infrared photography was more useful for delineating dispersion, but that either type could be used for both tasks. Transparencies at a scale of 1:5 000 were adequate for locating many sources of pollution, while a scale of 1:10 000 revealed dispersion patterns (Welch 1971).

In 1972, Rudder et al. developed a photographic and non-photographic aerial surveillance system for detecting actual and potential oil spills from oil refineries and industrial sites located along the Mississippi River. Spills, effluents and waste areas were identifiable on multispectral imagery.

In 1974, the U.S. Environmental Protection Agency conducted an airborne remote sensing study to monitor warm-water discharges and other industrial effluents from various sites into Lake Erie and the Detroit and St. Clair Rivers. Aerial thermography and ground data were used in studying the thermal properties of dispersion plumes from 18 power plants and 11 industrial sites (Environmental Protection Agency 1974).

Thermography is an ideal means of monitoring plumes of ''hot'' water in lakes and rivers from industrial and power stations which use the water as a coolant, and of mapping the dispersion of the discharges. Thermography has also been used successfully in the mapping of oil spills, as the result of a contrast in temperature between the oil-covered surface and open water (Ellis and Senese 1981).

The Michigan Water Resources Commission found colour infrared aerial photography, aerial thermography and LANDSAT imagery valuable in monitoring waste water discharges from industrial and power plants along the Michigan shoreline of the St. Clair River, particularly when recorded during the winter months (Christensen and Wezernak 1975).

Fukue et al. (1981) used normal colour photography to study discharges from rivers into a bay in Japan, both at times of normal precipitation and during periods of unusually heavy rainfall. The photography was taken from a platform on a mountain top. The results demonstrated that river clarity or turbidity could be successfully monitored on colour film, with the aid of supplementary ground data.

Several studies have been conducted using LANDSAT imagery and digital data to monitor water quality. LANDSAT MSS band 5 (the red band) proved valuable in monitoring turbidity resulting from the Ogoki River diversion project in Northwestern Ontario (Ontario Centre for Remote Sensing 1977). Schiebe et al. (1983) used the first four LANDSAT TM bands to provide information on concentrations of suspended sediments in surface waters in the lower Mississippi River floodplain.

Several other airborne scanners, such as fluorosensors and the Ocean Colour Scanner, have been employed in detecting and monitoring various water quality parameters.

The fluorosensor illuminates a target within a specific wavelength of ultraviolet light. Many substances, such as algae and other aquatic plant life on or near the surface, fluoresce at characteristic wavelengths. Oil spills can be detected and classified according to the same principle.

Experiments conducted on the Ottawa River near Hawkesbury, Ontario showed that the measurement of fluorescence from aircraft are effective in the monitoring of effluents from pulp and paper mills. During the pulp ''cooking'' process, lignosulphonates are extracted and discharged into rivers. When these organic materials decompose, they rob the water of oxygen, thus seriously harming fish populations. The organic materials are highly fluorescent and can thus be readily detected and mapped using a fluorosensor (Harper 1983).

The Ocean Colour Scanner is a non-photographic sensor which is effective in detecting suspended sediments. Khorram (1981) used the scanner to monitor water quality in the delta of San Francisco Bay, and found that it detected pollutants which had not been detected by either colour or colour infrared photography.

Studies of Dam Sites and Reservoirs

Numerous remote sensing studies have been conducted of dam sites and reservoirs. Mollard and Dishaw (1966), Mollard and Carr (1973) and Verdin (1985) have used various sensors to acquire data for dam site planning and for monitoring drainage flow, water quality and bank erosion in reservoirs. Airphoto interpretation was used to map the local and regional terrain conditions around a number of hydroelectric sites in western Canada. The study included the factors of slope stability, bank height and ground water/surface discharge. The digital classification of LANDSAT data has also proven effective for mapping and monitoring reservoirs (Mollard and Carr 1973).

Satellite data have also been used to monitor water quality in large river reservoirs and estuaries. In a 1976 study, sensors in both satellites and aircraft were tested to determine the optimum wavelength ranges for monitoring suspended sediments in six northern Mississippi River reservoirs (Ritchie et al. 1976). In two 1985 studies, one in Utah and Wyoming and the other in North Carolina, LANDSAT data were combined with surface measurements to provide a very good quantitative assessment of water quality (Verdin 1985 and Khorram 1985). Verdin's study used LANDSAT data for estimating trophic conditions such as water clarity and chlorophyll concentrations in a reservoir.

In 1985, the Federal Institute of Waterways in West Germany monitored dams along rivers using multispectral and multitemporal data from an airborne sensor. A thematic map of soil moisture anomalies was produced for the dam itself and the area surrounding it (Daedalus Enterprises Inc. 1985).

Habitat Analysis

Research into the use of remote sensing techniques to study the habitat of various fish species has increased in recent years. Remote sensing is particularly valuable in monitoring the degradation or rehabilitation of river environments. Ulliman et al. (1982) was able to estimate sediment loadings in a river in Idaho from the study of both black and white and colour airphoto coverage combined with ground data. The sediments, which originated in erosion from road construction and logging activities, were causing severe habitat change in salmon and trout spawning areas. Historic black and white airphotos were compared to current photo coverage to permit the detection of changes over time. The study illustrated the effectiveness of aerial photography for investigating clearwater streambed sediments and for predicting future trends as an aid to river management. Hagen et al. (1977) demonstrated the usefulness of medium-scale colour infrared aerial photography for terrestrial and aquatic habitat mapping in the upper Mississippi River.

Site-Specific Investigations using Large-Scale Remote Sensing Data

Large-scale airborne and spaceborne remote sensing systems can be applied to the relatively detailed study of water quality, the assessment of riverbanks and habitat, and the sampling of fish populations. Airborne sensors provide a more appropriate resolution than spaceborne sensors for this type of study, while offering a significant cost savings over the use of intensive field study on its own.

Localized Water Quality Studies

The assessment and monitoring of water quality includes the study of suspended sediments, pollutants and aquatic vegetation. Low-altitude aerial photography using black and white, colour or colour infrared films is the best method of recording these features.

Bhargava (1983) analyzed black and white photographs with a spectrophotometer to investigate photographic optical density for water. The photographs used in the study were taken from a distance of 3 m above the target. The study determined that photographic optical density could be correlated with turbidity and also with biochemical oxygen demand — both important indicators of water pollution.

McKim et al. (1984) found that data from an airborne spectroradiometer provided qualitative and quantitative information on suspended sediments.

Lo (1976) used aerial photography recorded in 1956 and 1975 to detect sources of pollution in a channel in Hong Kong and to identify the types of polluting substances.

In 1972, Welch et al. demonstrated an aerial surveillance system for pollution control based on aerial photography. Medium-scale colour infrared coverage was used to classify land use in areas where potential pollution spill sources existed. Large-scale colour photography was then used to monitor individual sites. Flannery (1983) also used colour and colour infrared aerial photography to pinpoint 26 out of 27 existing outfalls on a river in Ohio.

Ultraviolet photography can be used to detect surface oil films, but requires good daylight and a minimum of atmospheric haze to be effective. This photography is best recorded at altitudes less than 3 000 m.

Colour infrared photography is normally the most effective sensor for the identification of emergent aquatic vegetation. Healthy aquatic plants generally appear in tones of red and pink which contrast sharply with the black colour of the water. When the chlorophyll content of aquatic plants is reduced, the vegetation appears on the photographs in colours abnormal for the species. The presence of water pollution is one possible cause of this phenomenon; thus, the colour of aquatic vegetation on colour infrared photography can serve as an indicator of water quality.

Riverbank and Fish Habitat Assessment.

The same remote sensing techniques used in water quality studies can be used to assess and monitor riverbank stability, conduct habitat studies, assess stream shading and detect river-flow obstructions.

Singhroy and Wightman (1981) used large-scale colour and colour infrared aerial photography as well as thermography to monitor bank erosion along the Annapolis River of Nova Scotia. Potentially unstable areas were successfully identified, as well as areas of bank erosion and sedimentation.

Photographic remote sensing techniques are used to monitor stream habitats of various fish species. Increases in sediment load caused by man-made bank erosion can change the aquatic environment and impair the respiration of fish and other aquatic organisms with gills. The increased turbidity also blocks out sunlight, thus reducing photosynthesis in aquatic plants and algae (Singhroy and Moncrieff 1984). In a study conducted in the Thames River in southern Ontario, normal colour and colour infrared photography showed the degree of disturbance and the extent of the downstream dispersion of sediments caused by pipeline construction. This photography was also used to monitor the restoration of natural vegetation along the riverbanks after construction had been completed (Singhroy and Moncrieff 1984).

Best (1982) reviewed the work of several researchers (Cuplin 1978a, 1978b; Greentree and Aldrich 1976, 1978; Hagen et al. 1977; Minor et al. 1977) who evaluated the use of colour and colour infrared photography at various scales in assessing and monitoring river habitat. Colour photography was found to be best for evaluating river bank conditions and bottom types, while colour infrared photography was best for assessing aquatic vegetation. Both were successfully used to monitor water quality.

Colour video cameras have also been used for monitoring fish habitat. Overton and Mussakowski (1983) developed a method for applying low-altitude colour video recording to the mapping of trout stream habitats in southern Ontario. Under this method, the video system was operated from a helicopter flying at 40 m above the river surface. The colour video provided a permanent record of changes in trout habitat. While offering some of the same advantages as colour aerial photography, it offered the additional advantages of instantaneous viewing and quick access to data stored on cassettes. Other applications of the airborne video technique include the monitoring of aquatic vegetation, spawning areas and stream dimensions. Improvements are needed in video resolution and colour to improve the information content and interpretability of video data (Mussakowski 1984).

Survey and Inventory of Fish Populations

The development of new remote sensing technologies has provided direct and indirect methods for fish survey and inventory. The direct approach normally involves detection and enumeration of the fish, while the indirect approach usually involves remote measurements of environmental parameters. Historically, aerial photography has been the chief method of surveying fish populations (Kelez 1947; Eicher 1953). Recent developments in electronic and optical sensors have provided researchers with better detection and monitoring methods. These new sensors allow instantaneous detection, but also provide photographic or digital records for further study. Most of the research has been done on salmon and pelagic fish species; the use of these methods for fish population surveys in inland waters is relatively new (Cheney and Rabanal 1984).

The direct detection of fish using remote sensing techniques has its most important application in locating fish for commercial and recreational purposes. Spotters and researchers use real-time visual detection, aerial photography and electronic sensors for this purpose.

Spotters operate from aircraft flown at altitudes of from 150 to 950 m. Their function is to maintain radio contact with fishing vessels and direct them toward schools of fish. On the basis of subtle differences in colour and light intensity, the spotters locate the schools and identify the species from colour, behaviour, shape and size (Squires 1972).

Aerial photography can be used to study the distribution and relative abundance of pelagic fish species. Clear, cloudless skies are needed for recording photography for fisheries studies. High sun angles which produce sun glint in the photographs are undesirable, as are low sun angles which limit the light available for photography. It has been determined that an increase in exposure of as much as 2.5 f-stops above ordinary terrestrial exposure values is needed for maximum water penetration and the detection of pelagic fish schools (Johnson and Munday 1983).

There is no single camera format and film/filter combination which provides optimum photographic coverage for all fish surveys. The coverage most widely used has been 22.8 × 22.8 cm (9 × 9 inch) format colour or colour infrared photography taken with a 15.2 cm (6 inch) lens. Kelez (1947) and Eicher (1953) used large-format aerial photography to determine the size of spawning red salmon in Alaska. Eicher employed a large-format orthochromatic film to provide depth penetration and contrast between the red fish and the river bottom. The effective film speed was increased by the use of different yellow-green and polarizing filters, depending on the composition of the stream bottom. The photography was taken over known spawning areas, and the counts of fish were used as an index of abundance. The study concluded that the use of vertical aerial photos improved the accuracy of fish counting, especially in the case of large schools, and was less costly than on-site counts. In 1975, 70 mm-format film was used to detect tuna at depths of 10–15 m in the Bahamas. Both the blue and green bands of the spectrum provided good information; however, the green band demonstrated better contrast. The principal advantage of aerial photography over other survey techniques is that large-area coverage can be acquired at a nominal cost (Johnson and Munday 1983).

Photographic interpretation should be used with caution, however, for calculating fish biomass. Only a few studies have shown a direct relationship between the surface area of a school and fish biomass (Stevenson and Pastula 1971).

An alternative surveying method involves the use of the known spectral reflectivity of various fish species. Various film and filter combinations can be used to enhance reflectivity and allow the detection of particular species. A 1968 study found differences in spectral reflectivity among 15 species tested (Johnson and Munday 1983). In 1971, Stevenson and Pastula were successful in distinguishing among three species of pelagic schooling fish on the basis of their spectral signatures.

Recent advances in high-power, pulsed airborne laser systems operating in the blue-green portion of the visible spectrum indicate that they may be useful in fisheries applications. Computer simulations show that a 2000-Kw laser system, scanning a 75 m swath, can detect fish at a depth of 16 m, from an altitude of approximately 1700 m (Johnson and Munday 1983). Vanselous and Kemmerer (1975) indicated that advances in laser technology would have application to fish inventory, as a laser sensor could be operated both day and night and could penetrate water for the possible detection, quantification and identification of fish schools.

An indirect method of surveying fish populations is through monitoring fishing vessels. Visual reconnaissance and aerial photography have been used to count fishing villages, canoes and other evidence of fishing activities on river and lake systems in Africa. Such surveys have been useful for estimating the intensity of fishing and obtaining information on the movements of local fishing fleets. The surveys were usually supported by ground-truth data in the form of inspections of the catch carried out at the time of the overflight (Howard and Welcomme 1977). Airborne synthetic aperture radar has also been used for the surveillance of fishing vessels. Digitally processed radar data demonstrated that vessels could be reliably detected and located from measurements of speed and direction. The current emphasis of studies in this field is on the use of airborne radar sensors in classifying vessels (Johnson and Munday 1983).

The efficiency of using airborne sensors for fish detection has been extensively documented. As early as 1967, it was stated that aerial surveys were two-and-a-half times more efficient than conventional surveys in locating schools of tuna (Jones and Sund 1967). In the intervening years, however, remote sensing techniques have not been implemented operationally for this purpose to any significant degree.

Conclusion

Remote sensing techniques have proven valuable for a broad range of water resource applications. Extensive research has shown that remote sensing can provide data essential to the inventory, assessment and monitoring of rivers and river systems. Remote sensing techniques offer the advantage of acquiring data from ranges of the electromagnetic spectrum other than the visible, and furnish a permanent record for verification and historical reference. Furthermore, in appropriate applications, they are generally more cost-effective than surface survey and sampling methods.

In planning-level studies designed to search large areas for sites requiring intensive analysis, remote sensing has emerged as a rapid and economical alternative to traditional methods.

At the regional level, repetitive synoptic data such as LANDSAT imagery permits the study of extensive hydrologic features over time. The information derived from this imagery on land cover, snow cover and the extent of floods is useful in storm water management planning, the analysis of drainage basin and channel networks, and the identification and area calculation of land cover classes that influence watershed runoff.

At the intermediate level, both airborne and spaceborne remote sensing data have been employed in applications ranging from floodplain mapping and water quality monitoring to river system habitat analysis. Assessing and monitoring rivers at the intermediate scale may require a combination of remote sensing data acquisition and ground data collection and analysis.

At the site-specific scale, aircraft sensors are generally preferable for the level of detail they provide. Applications of site-specific data include localized water quality studies, riverbank and fish habitat assessment, and the survey and inventory of fish populations. The role of remote sensing at this level is to complement on-site investigations. The combination of remote sensing and field data collection provides the hydrologist and water resource manager with a powerful tool, one which cannot be used successfully without a precise understanding of the inherent advantages and limitations of the remote sensing technology.

Remote sensing techniques are not yet applied as widely as their advantages would suggest. One reason is the fact that potential applications are not widely known or their significance understood. Only the cooperative efforts of water resources personnel and remote sensing specialists can overcome this barrier.

References

BEST, R. G. 1982. Handbook of remote sensing in fish and wildlife management. Remote Sensing Institute, South Dakota State University, Publ. SDSU-RSI-82-05, Brooking, SD 57007. 44 p.

BHARGAVA, D. S. 1983. Very low altitude remote sensing of the water quality or rivers. Photogram. Eng. Remote Sens. 49(6): 805–809.

CHENEY, D. P., AND H. R. RABANAL. 1984. Remote sensing and its application to inland fisheries and aquaculture. FAO Fish. Circ. 768: 50 p.

CHRISTENSEN, R. J., AND C. T. WEZERNAK. 1975. Use of remote sensing for water resource management in Michigan. Proc. Int. Symp. Remote Sens. Environ. Vol. 1, Ann Arbor, MI. 10: 485–494.

COLWELL, R. N. [ed.]. 1983. Manual of remote sensing. 2nd ed., 2 vol., American Society of Photogrammetry, Falls Church, VA. 22046, 2440 p.

CUPLIN, P. 1978a. Remote sensing streams. Proceedings, Integrated Inventories of Renewable National Resources. USDA Forest Service, Gen. Tech. Rep. RM-55, Tucson, AZ.: 257–259.

1978b. The use of large scale colour infrared photography for stream habitat inventory. Proceedings, Pecora IV Symposium: Application of Remote Sensing Data to Wildlife Management. Natl. Wildl. Fed. Sci. Tech. Ser. 3: 207–211.

DAEDALUS ENTERPRISES INC. 1985. Scanner applications ... worldwide, 1985 compendium. Ann Arbor, MI 48106. 28 p.

DEUTSCH, M., AND F. RUGGLES. 1974. Optical data processing and projected applications of the ERTS-1 imagery covering the 1973 Mississippi River Valley floods. Water Resour. Bull. 10(5): 1023–1039.

DRAEGER, W. C. 1977. Monitoring irregated land acreage using LANDSAT imagery, an application example. Proc. Int. Symp. Remote Sens. Environ. Vol. 1, Environmental Research Institute of Michigan, Ann Arbor, MI. 11: 515–524.

EICHER, G. J. (JR.). 1953. Aerial methods of assessing red salmon populations in western Alaska. J. Wildl. Manage. 17: 521–527.

ELLIS, T. J., AND E. M. SENESE. 1981. Remote sensing in pollution abatement. Proc. Ontario Industrial Waste Conference. Toronto, Ont. 28: 245–252.

ENVIRONMENTAL PROTECTION AGENCY. 1974. Remote sensing study of steam-electric power plant thermal discharges to Lake Erie and the Detroit and St. Clair Rivers, Ohio and Michigan. Environmental Protection Agency, Office of Enforcement, National Field Investigations Centre — Denver, Colorado and Region V, Chicago, Illinois. 61 p.

ESTES, J. E., J. R. JENSEN, L. R. TINNEY, AND M. RECTOR. 1975. Remote sensing inputs to water demand modelling. Proc. NASA Earth Resources Survey Symp.: 2585–2620.

FLANNERY, J. J. 1983. Applications of remote sensing in industrial analysis, p. 401–422. *In* B. F. Richason [ed.] Introduction to Remote Sensing of the Environment, 2nd Edition. Kendall/Hunt Publishing Company, Dubuque, IA.

FUKUE, K., H. SHIMODA, AND T. SAKATA. 1981. River discharge monitoring using aerial colour photography. J. Soc. Photogram. Sci. Technol. Jpn. 44(4): 295–302.

GREENTREE, W. J., AND R. C. ALDRICH. 1976. Evaluating stream trout habitat on large-scale aerial colour photographs. USDA Forestry Service, Research Paper PSW-123, Pacific SW Forest and Range Experimental Station, Berkeley, CA. 21 p.

1978. Measuring trout habitat as an indication of population on large scale aerial colour photographs. Proceedings, Pecora IV Symposium: Application of Remote Sensing Data to Wildlife Management. Natl. Wildl. Fed. Sci. Techn. Ser. 3: 65–71.

HAGEN, R., L. WERTH, AND M. MEYER. 1977. Upper Mississippi River habitat inventory — Phase I, 1:24 000 CIR cover type mapping, Guttenberg, IA to Cairo, IL. University of Minnesota, College of Forestry, IAFHE RSL Research Report 77-5, St. Paul, MN. 32 p.

HALLBERG, G. R., B. E. HOYER, AND A. RANGO. 1973. Application of ERTS-1 imagery to flood inundation mapping. Proc. Symp. on Significant Results Obtained from ERTS-1, Volume II-Summary of Results. X-650-73-127. New Carrollton, MD.: 51–70.

HARPER, D. 1983. Eye in the sky, introduction to remote sensing, 2nd ed. Canada Science Series Multiscience Publication Limited, Montreal, Quebec, in association with Energy, Mines and Resources. 252 p.

HELLER, R. C., AND K. A. JOHNSON. 1979. Estimating irrigated land acreage from LANDSAT imagery. Photogram. Eng. Remote Sens. 45(10): 1379–1386.

HOWARD, J. A., AND R. L. WELCOMME. 1977. FAO and remote sensing applied to fisheries, p. 27-37. *In* Aerial and Spatial Remote Sensing and Marine Living Resources: Present and Future Possibilities. Eurocean, Monaco-ville (Monaco).

JENSEN, J. R., M. E. HODGSON, E CHRISTENSEN, H. E. MACKEY, JR., L. R. TINNEY, AND R. SHARITZ. 1986. Remote sensing inland wetlands: A multispectral approach. Photogram. Eng. Remote sens. 52(1): 87–100.

JOHNSON, R. W., AND J. C. MUNDAY, JR., [(ed]. 1983. The marine environment, p. 1371–1496. *In* R. N. Colwell [ed.] The manual of remote sensing, Vol. 2. American Society of Photogrammetry, Falls Church, VA 22096.

JONES, A. C., AND P. N. SUND. 1967. An aircraft and vessel survey of surface tuna schools in the Lesser Antilles. Comm. Fish. Rev. 29(3): 41–45.

KELEZ, G. B. 1947. Measurement of salmon spawning by means of aerial photography. Pac. Fisherman. 45(3): 49–51.

KHORRAM, S. 1981. Use of ocean colour scanner data in water quality mapping. Photogram. Eng. Remote Sens. 47(5): 661–676.

1985. Remote sensing of water quality in the Neuse River Estuary, North Carolina. Photogram. Eng. Remote Sens. 51(3): 329–341.

LAWRENCE, G. R., D. WHITE, AND I. DESLAURIERS. 1980. The detection of groundwater discharges (springs) using aerial thermography. Proc. Canadian Symposium on Remote Sensing. Halifax, N.S. 6: 483–491.

LO, C. P. 1976. Photographic analysis of water quality changes. Photogram. Eng. Remote Sens. 43(3): 309–315.

MARTINEC, J. 1980. Hydrological basin models, p. 447–459. *In* G. Fraysse [ed.] Remote Sensing Application in Agriculture and Hydrology. Published for the Commission of the European Communities, Directorate General Scientific and Technical Information and Technical Management, Luxenbourg, A.A. Balkema/Rotterdam.

McKim, H. L., C. J. Merry, and R. W. Layman. 1984. Water quality monitoring using an airborne spectroradiometer. Photogram. Eng. Remote Sens. 50(3): 353–360.

Minor, J., L. Caron, and M. Meyer. 1977. Upper Mississippi River habitat inventory — Phase III, detailed mapping of upland, marsh, emergent aquatic and submergent vegetation from 1:9 600 CIR aerial photography, Hastings, MN to Guttenberg, IA. University of Minnesota College of Forestry, St. Paul. MN. IAFHE RSL Research Report 77-7: 24 p.

Mollard, J. D., and H. E. Dishaw. 1966. Applications of airphoto interpretation in hydro-electric power investigations in western Canada. The Eng. J. April 1966: 3–11.

Mollard, J. D., and P. A. Carr. 1973. Applications of the ERTS-1 satellite in remote sensing of water resources data in Canada. Symposium, COSPAR, XVIth Plenary Meeting and Related Symposia. Konstanz, West Germany.

Morrison, R. B., and M. E. Cooley. 1973. Assessment of flood damage in Arizona by means of ERTS-1 imagery. Proc. Symposium on Significant Results Obtained from ERTS-1, Volume 1. New Carrollton, MD.: 755–760.

Mussakowski, R. 1984. The application of video remote sensing to resource surveys and environmental monitoring. Proc. Canadian Symposium on Remote Sensing. Montreal, Quebec 8: 91–99.

Ontario Centre For Remote Sensing. 1977. The impact of the Ogoki diversion on the erosion of the Little Jackfish River and on the turbidity of Ombabika Bay. Prepared for the Regional Development Branch, Ministry of Treasury, Economics and Intergovernmental Affairs. Toronto, Ont. 65 p.

1979. Annual Review, 1978–1979. Ministry of Natural Resources, Queen's Park, Toronto, Ont.

1983. An evaluation of narrow-band low-light-level television (LLLTV) for the airborne tracking of fluorescent dye releases used in waste assimilation studies. Prepared for the Water Resources Branch, Ministry of the Environment. Toronto, Ont. 11 p.

Overton, J., and R. S. Mussakowski. 1983. Stream habitat evaluation using colour video recording techniques from a helicopter. Prepared for Fisheries Branch, Ministry of Natural Resources, by the Ontario Centre for Remote Sensing, Ministry of Natural Resources, Toronto, Ont. 27 p.

Parry, J. T., and H. Turner. 1971. Infrared photos for drainage analysis. Photogram. Eng. Remote Sens. 37(10): 1031–1038.

Pokrant, H., and W. Hildebrand. 1984. Remote sensing to assess land use and land cover changes affecting a fishery resource in southwestern Manitoba. Proc. Canadian Symposium on Remote Sensing. Montreal, Quebec 8: 405–412.

Ragan, R. M., and V. V. Salomonson. 1978. The definition of hydrologic model parameters using remote sensing techniques. Proc. International Symposium on Remote Sensing of Environment. Manila, Philippines, 12: 481–495.

Rango, A. 1975. Applications of remote sensing to watershed management. Proceedings of the ASCE Irrigation and Drainage Division Symposium on Watershed Management. Logan, Utah: 700–714.

Rango, A., and V. V. Salomonson. 1973. Repetitive ERTS-1 observations of surface water variability along rivers and other low-lyingh areas. Proceedings, AWRA International Symposium on Remote Sensing and Water Management. Burlington, Ontario, 191–208.

Rango, A., and A. T. Anderson. 1974. Flood hazard studies in the Mississippi River basin using remote sensing. Bull. Water Resour. 10(5): 1060–1081.

Rango, A., and P. O'Neill. 1982. Effective watershed management using remote sensing technology, p. 301–308. *In* C. J. Johannsen and J. L. Sanders [ed]. Remote sensing for resource management. Soil Conversation Society of America, Ankeny, IA.

Ritchie, J. C., F. R. Schiebe, and J. R. McHenry. 1976. Remote sensing of suspended sediments in surface waters. Photogram. Eng. Remote Sens. 42(12): 1539–1545.

Robinove, C. [undated.] The role of remote sensing and satellite monitoring systems in hydrologic hazard management. U.S. Geol. Surv. Reston, VA. 5 p.

Rogers, R. H., L. E. Reed, N. F. Schmidt, and T. G. Mara. 1975. LANDSAT-1: automated land-use mapping in lake and river watersheds. Prepared for the ASP-ACSM Fall Convention, Phoenix, AZ, 13 p.

Rudder, C. L., C. J. Remheimer, and J. L. Berrey. 1972. Aerial surveillance spill prevention system. Office of Research and Monitoring Environmental Protection Technology Series, U.S. Environmental Protection Agency, Washington, D. C. 20460. EPA-RS-72-007: 112 p.

Sabins, F. F. (Jr.) 1978. Remote sensing principles and interpretation (first edition), W. H. Freeman and Company, San Francisco, CA. 426 p.

1987. Remote sensing principles and interpretation (second edition). W. H. Freeman and Company, New York, NY. 449 p.

Salomonson, V. V. [ed.]. 1983. Water resources assessment, p. 1497–1570. *In* R. N. Colwell [ed.] Manual of remote sensing, Vol. 2. American Society of Photogrammetry, Falls Church, VA.

Schiebe, F. R., J. C. Ritchie, and G. O. Boatwright. 1983. A first evaluation of LANDSAT TM data to monitor suspended sediments in lakes. Proceedings of the LANDSAT-4 Science Characterization Early Results Symposium, Volume IV: Applications. NASA Goddard Space Flight Center, Greenbelt, Maryland, NASA Conference Publication 2355: 337–347.

Sears, S. K. 1985. Remote sensing pilot project technical evaluation. Environmental Studies and Assessments Department, Ontario Hydro, Toronto, Ont. Rep. 85262: 40 p.

Singhroy, V., and J. F. Wightman. 1981. Bank erosion and floodplain studies of the Annapolis River: an application of remote sensing data. Proceedings, 7th Canadian Symposium on Remote Sensing. Winnipeg, Man.: 304–315.

Singhroy, V., and I. Moncrieff. 1984. Applications of remote sensing to pipeline construction in Ontario. Proceedings, Facility Siting and Routing '84. Energy and Environment, Banff, Alta.: 329–351.

Sollers, S. C., A. Rango, and D. L. Henninger. 1978. Selecting reconnaissance strategies for floodplain surveys. Bull. Water Resour. 14(2): 359–373.

Squire, J. L. 1972. Apparent abundance of some pelagic marine fishes of the southern and central California coast as surveyed by an airborne monitoring program. Dep. Comm. Fish. Bull. 70(3): 1005–1019.

Stevenson, W. H., and E. J. Pastula. 1971. Observations on remote sensing in fisheries. Comm. Fish. Rev. 33(9): 9–21.

Still, D. A., and S. F. Shih. 1985. Using LANDSAT data to classify land use for assessing the basinwise runoff index. Water Resourc. Bull. Am. Water Resour. Assoc. 6: 931–940.

Thiruvengadachari, S. 1981. Satellite sensing of irrigated lands in semi-arid areas: an India study. Photogram. Eng. Remote Sens. 48(10): 1493–1499.

Ulliman, J. J., H. Singh, and W. Megahan. 1982. Remote sensing detection for planning on the Salmon River. Proceedings of the 1982 Convention of the Society of American Foresters. Cincinnati, OH.: 133–137.

Vanselaus, T. M., and A. J. Kemmerer. 1975. An overview of remote sensing applications to fisheries related problems. Proc. Symposium on the Utilization of Remote Sensing Data in the Southeastern United States. Athens, GA.: 13–24.

VERDIN, J. P. 1985. Monitoring water quality conditions in a large western reservoir with LANDSAT imagery. Photogram. Eng. Remote Sens. 51(3): 343–353.

WELCH, R. I. 1971. Remote sensing for water pollution control. Photogram. Eng. Remote Sens. (Photogrammetric Brief). 37(12): 1285–1286.

WELCH, R. I., A. D. MARMELSTEIN, AND P. M. MAUGHAN. 1972. A feasibility demonstration of an aerial surveillance spill prevention system. Office of Research and Monitoring, Water Pollution. Environmental Protection Agency, Washington, D.C. 20460, Central Research Series 15080H0L01/72: 120 p.

YATES, H., A. STRONG, D. MCGINNIS JR., AND D. TARPLEY. 1986. Terrestrial observations from NOAA operational satellite. Science. January 31, 1986: 463–470.

The Flood Pulse Concept in River–Floodplain Systems

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Abstract

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The principal driving force responsible for the existence, productivity, and interactions of the major biota in river-floodplain systems is the flood pulse. A spectrum of geomorphological and hydrological conditions produces flood pulses, which range from unpredictable to predictable and from short to long duration. Short and generally unpredictable pulses occur in low-order streams or heavily modified systems with floodplains that have been leveed and drained by man. Because low-order stream pulses are brief and unpredictable, organisms have limited adaptations for directly utilizing the aquatic/terrestrial transition zone (ATTZ), although aquatic organisms benefit indirectly from transport of resources into the lotic environment. Conversely, a predictable pulse of long duration engenders organismic adaptations and strategies that efficiently utilize attributes of the ATTZ. This pulse is coupled with a dynamic edge effect, which extends a "moving littoral" throughout the ATTZ. The moving littoral prevents prolonged stagnation and allows rapid recycling of organic matter and nutrients, thereby resulting in high productivity. Primary production associated with the ATTZ is much higher than that of permanent water bodies in unmodified systems. Fish yields and production are strongly related to the extent of accessible floodplain, whereas the main river is used as a migration route by most of the fishes.

In temperate regions, light and/or temperature variations may modify the effects of the pulse, and anthropogenic influences on the flood pulse or floodplain frequently limit production. A local floodplain, however, can develop by sedimentation in a river stretch modified by a low head dam. Borders of slowly flowing rivers turn into floodplain habitats, becoming separated from the main channel by levées.

The flood pulse is a "batch" process and is distinct from concepts that emphasize the continuous processes in flowing water environments, such as the river continuum concept. Floodplains are distinct because they do not depend on upstream processing inefficiencies of organic matter, although their nutrient pool is influenced by periodic lateral exchange of water and sediments with the main channel. The pulse concept is distinct because the position of a floodplain within the river network is not a primary determinant of the processes that occur. The pulse concept requires an approach other than the traditional limnological paradigms used in lotic or lentic systems.

Résumé

JUNK, W. J., P. B. BAYLEY, AND R. E. SPARKS. 1989. The flood pulse concept in river-floodplain systems, p. 110–127. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Les inondations occasionnées par la crue des eaux dans les systèmes cours d'eau-plaines inondables constituent le principal facteur qui détermine la nature et la productivité du biote dominant de même que les interactions existant entre les organismes biotiques et entre ceux-ci et leur environnement. Ces crues passagères, dont la durée et la prévisibilité sont variables, sont produites par un ensemble de facteurs géomorphologiques et hydrologiques. Les crues de courte durée, généralement imprévisibles, surviennent dans les réseaux hydrographiques peu ramifiées ou dans les réseaux qui ont connu des transformations importantes suite à l'endiguement et au drainage des plaines inondables par l'homme. Comme les crues survenant dans les réseaux hydrographiques d'ordre inférieur sont brèves et imprévisibles, les adaptations des organismes vivants sont limitées en ce qui a trait à l'exploitation des ressources de la zone de transition existant entre le milieu aquatique et le milieu terrestre (ATTZ), bien que les organismes aquatiques profitent indirectement des éléments transportés dans le milieu lotique. Inversement, une crue prévisible de longue durée favorise le développement d'adaptations et de stratégies qui permettent aux organismes d'exploiter efficacement l'ATTZ. Une telle crue s'accompagne d'un effet de bordure dynamique qui fait en sorte que l'ATTZ devient un «littoral mobile». Dans ces circonstances, il n'y a pas de stagnation prolongée et le recyclage de la matière organique et des substances nutritives se fait rapidement, ce qui donne lieu à une productivité élevée. La production primaire dans l'ATTZ est beaucoup plus élevée que celle des masses d'eau permanentes dans les réseaux hydrographiques non modifiés. Le rendement et la production de poissons sont étroitement reliés à l'étendue de la plaine inondable, tandis que le cours normal de la rivière est utilisé comme voie de migration par la plupart des poissons.

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Dans les régions tempérées, les variations de l'ensoleillement et/ou de la température peuvent modifier les effets de la crue, et l'action de l'homme sur la crue des eaux et sur les plaines inondables limite souvent la production. Une plaine inondable peut cependant se former localement par sédimentation dans un tronçon de cours d'eau modifié par un barrage de basse chute. Aussi, les rives des cours d'eau à faible débit se transforment en plaines inondables suite à la formation de levées alluviales qui les séparent du canal principal.

Les crues sont des phénomènes qui se manifestent par à-coups. Cette situation est différente de celles prises en compte par les concepts qui mettent l'accent sur les processus continus intervenant dans les eaux courantes, tel que le concept du continuum appliqué aux cours d'eau. Les plaines inondables constituent un cas particulier car elles ne sont pas tributaires de la transformation inefficace de la matière organique en amont, même si leur réserve d'éléments nutritifs dépend en partie des échanges latéraux périodiques d'eau et de sédiments avec le canal principal. La crue est un phénomène particulier par rapport aux conditions normales parce que la position d'une plaine inondable dans le réseau fluvial n'est pas un facteur qui détermine de façon fondamentale les processus observés dans ce type de milieu. Les questions soulevées par le phénomène des crues ne peuvent pas être résolues à l'aide des concepts traditionnels de la limnologie utilisés pour étudier les systèmes lotiques et lénitiques.

Hydrologists think of rivers as links in the hydrological cycle, which transport runoff water from the continents to the sea or to the center of endorheic basins (Curry 1972). Since water is a good solvent and flowing water provides kinetic energy, water transport by rivers is linked with the transport of dissolved and solid substances. However, precipitation and river discharge typically vary significantly during the annual cycle. At low discharge rates, rivers flow in well-defined channels, but at high water in natural systems wide floodplains are recurrently inundated.

River-floodplain systems provide important habitats for biota, and ecologists have tried to link the biota of river systems with local environmental conditions and to adopt existing paradigms from other aquatic systems. These attempts have met with two problems: (1) the division of ecology into terrestrial ecology and limnology; and (2) the classification of water bodies into more or less closed, lentic systems with accumulating characteristics (lakes, ponds) as outlined in traditional limnology texts (Ruttner 1952) and open, lotic systems with discharging characteristics (streams, rivers) (Hynes 1970). The transient nature of aquatic habitats in floodplains resulted in biased treatment or in their omission. When studying rivers, most limnologists restricted themselves to river channels; when studying floodplains, they concentrated on floodplain lakes, often treating them as classical lakes.

One recent theoretical construct in river ecology, the river continuum concept (RCC) (Vannote et al. 1980), is based on the hypothesis that a continuous gradient of physical conditions exists from headwater to mouth. Analogous to the energy equilibrium theory of fluvial geomorphologists, the RCC states that structural and functional characteristics of stream communities are adapted to conform to the most probable position or mean state of the physical system. Producer and consumer communities establish themselves in harmony with the dynamic physical conditions of a given river reach, and downstream communities are fashioned to capitalize on the inefficiencies of upstream processing. Both upstream inefficiency (leakage) and downstream adjustment seem predictable. Therefore the RCC purports to provide a framework that permits us to integrate predictable and observable biological features of lotic systems (Vannote et al. 1980).

In our view, the RCC suffers from two basic limitations: (1) it was developed on small temperate streams but has been extrapolated to rivers in general; and (2) it was based on a concept that had been elaborated for the river basin in a geomorphological sense but was in fact restricted to habitats that are permanent and lotic.

Most papers that discuss the RCC recognize these limitations (Winterbourn et al. 1981; Barmuta and Lake 1982; Minshall et al. 1983; Minshall et al. 1985; Statzner and Higler 1985; Sedell et al. 1989) but fail to consider the biological significance of processes within the seasonal, aquatic habitats of floodplains. It may prove acceptable to modify the RCC to account for brief and unpredictable floods in low-order streams, even for catastrophic floods which change the physical environment and "reset" systems (Cummins 1977; Fisher 1983). However, as the size of a floodplain increases, usually along with increasing river discharge, the frequency of floods decreases, and their duration and predictability increase. These changes result in a distinct geomorphological and hydrological system with an increasing ratio of periodically lentic to lotic areas. This system results in adaptations of biota that are distinct from those in systems dominated by stable lotic or lentic habitats.

Recently, the importance of river-floodplains to fish populations in temperate, subtropical, and tropical regions has been shown by Lambou (1959), Holčík and Bastl (1976, 1977), Bryan and Sabins (1979), Welcomme (1979, 1985, 1989), Bayley (1980, 1981a, 1983), Junk (1980, 1984), and Littlejohn et al. (1985). These studies have signaled a renewed appreciation of pioneer work by Antipa (1911, 1928) and Richardson (1921). The status of the forest in subtropical river-floodplain systems has been summarized by Gosselink et al. (1981) and Wharton et al. (1981). The biases and inadequacies of limnological paradigms when applied to floodplain systems were recently discussed by Bayley (1980, 1983), Junk (1980, 1984), and Junk and Welcomme (1989) based on their experience in tropical systems. Amoros et al. (1986) and Bravard et al. (1986), who analysed the impact of flood regulation on plant and animal communities of the Rhône R. floodplain, stressed the importance of lateral and vertical dimensions of the river–floodplain system. Davies and Walker (1985) emphasized that considerable modification of the RCC was required before it could be applied to large river systems.

In this paper we synthesize evidence that suggests a complementary concept, the "flood pulse", that attempts to explain the relationship between the biota and the environment of an unmodified, large river–floodplain system. This concept is based on our experiences in relatively pristine systems in the neotropics and Southeast Asia and in the Upper Mississippi R. We derive this concept from the known ecology of typical biota that have adapted to the geomorphology and hydrology of large river–floodplain systems.

The Flood Pulse Concept

We propose that the pulsing of the river discharge, the flood pulse, is the major force controlling biota in river–floodplains. Lateral exchange between floodplain and river channel, and nutrient recycling within the floodplain have more direct impact on biota than the nutrient spiralling discussed in the RCC (Vannote et al. 1980). We postulate that in unaltered large river systems with floodplains in the temperate, subtropical, or tropical belt, the overwhelming bulk of the riverine animal biomass derives directly or indirectly from production within the floodplains and not from downstream transport of organic matter produced elsewhere in the basin.

The effect of the flood pulse on biota is principally hydrological. We postulate that if no organic material except living animals were exchanged between floodplain and channel, no qualitative and, at most, limited quantitative changes would occur in the floodplain (Bayley 1989). The relative importance of imported versus recycled inorganic nutrients in floodplains is not clear and probably varies between systems. Given similar hydrological conditions, the longitudinal position of a floodplain in the drainage network is of little importance with respect to the biota.

The Highway Analogy

Faunal life histories in unaltered large river–floodplains can be viewed as analogous to vehicles on a highway network. Were non-terrestrials to investigate this network, they would observe numerous bodies traveling in opposite directions and might well surmise that resources for those bodies were derived from the highways. If funds permitted a detailed study, it would reveal that four-wheeled creatures need to leave highways periodically for sustenance, along with their apparently symbiotic occupants. Eventually, major sources of production would be identified in farms, oil fields, and mines, vehicles consuming and distributing resources via the highway network as a response to production cycles and long-term economic changes.

The life histories of major plant and animal groups, in particular fish, in large river–floodplains are beginning to be understood sufficiently to contribute to the theory that the river network in a river–floodplain system is in many ways analogous to a highway network with the vehicles corresponding to the fish. Detritivores, herbivores, and/or omnivores support large fisheries in the main channel (Petrere 1978, 1982; Welcomme 1979; Quirós and Baigún 1985), but the highest yields are associated with adjoining floodplains (Richardson 1921; Lowe-McConnell 1964; Petrere 1983) and most of their production is derived from floodplain habitats (Welcomme 1979; Bayley 1983). The main channel is used principally as a route for gaining access to adult feeding areas, nurseries, spawning grounds, or as a refuge at low water or during winter in temperate zones. An analogous situation is found in large north-temperate and arctic rivers where most of the ichthyomass is anadromous; here the main feeding grounds are found in the delta area or in the sea (Grainger 1953; Andrews and Lear 1956; Foerster 1968; Roy 1989).

We will describe the functions of the floodplain and main channel in large river–floodplain systems with respect to the biota and evaluate the links between them and the nonfloodable watershed in the light of recent data.

Definition of a Floodplain

Terms applied to classical limnological and terrestrial systems can be inappropriate for explaining concepts in river–floodplains. This is not merely a semantic discussion because the classical terms are understood to define features and functions in their respective systems.

The "active floodplain" of a river is defined by North American hydrologists as the area flooded by a 100-year flood (Bhowmik and Stall 1979). This period is arbitrary, longer than most existing records, and has little ecological meaning. Bayley (1981b) noted that huge areas of shallow, very acidic, largely deoxygenated swamp occur in the Peruvian Amazon. These areas are distant from the main channels and inhospitable to the bulk of aquatic animals. He proposed an active floodplain that excluded these peripheral swamps in order to compare fish production and fishery yields among systems.

We define floodplains as "areas that are periodically inundated by the lateral overflow of rivers or lakes, and/or by direct precipitation or groundwater; the resulting physicochemical environment causes the biota to respond by morphological, anatomical, physiological, phenological, and/or ethological adaptations, and produce characteristic community structures". This ecological definition recognizes that flooding causes a perceptible impact on biota and that biota display a defined reaction to flooding. Furthermore, it implies that the impact of water level pulsing on biota is independent of the nature of its source and that there are many ecological similarities between floodplains adjacent to, for example, pulsing lakes or reservoirs and pulsing rivers. The definition encompasses a wide hydrological spectrum from short- to long-duration floods and from unpredictable to predictable timing. Our examples from large river systems exhibit predictable flood pulses of long duration.

We have termed the floodplain area the "aquatic/terrestrial transition zone" (ATTZ) because it alternates between aquatic and terrestrial environments. We use this term to stress our more specific definition of floodplain, because 'floodplain' has often been defined to include permanent lentic and lotic habitats. The inshore edge of the aquatic environment that traverses the floodplain (ATTZ) we have termed the "moving littoral". The floodplain or ATTZ has unique properties that have been considered to comprise a specific ecosystem (Junk 1980; Odum 1981).

Hydrologists consider the river and its floodplain as one unit since they are inseparable with respect to the water, sediment, and organic budgets. We term this unit the "river–floodplain system". Therefore, this system comprises permanent lotic habitats (main channels), permanent lentic habitats, and the floodplain (ATTZ). Many limnologists have difficulty defining floodplains viz a viz other aquatic systems, and they have defined artificial, stable borders between land and water. Conversely, floodplains are ecosystems with water boundaries that recurrently traverse large areas. The environmental change from the aquatic to the terrestrial phase at a specific point in a floodplain (ATTZ) may be as severe as the change from a lake to a desert. Classical limnological terms describing morphological features of lakes or rivers (e.g., shoreline, littoral, profundal, size, depth) are unsuitable and must be redefined or qualified, because they have become time-dependent in the floodplain. This time dependency is important because it affects the productive processes and the life cycles of plants and animals. Pieczyńska's (1972) definition of eulittoral appears to have functional parallels with our definition of a floodplain; however, the eulittoral occupied a very small part (±5 %) of the nonfloodplain lakes in her study and responded to a pulse amplitude of only about 40 cm. Also, we are cautious about drawing close parallels with the intertidal zone because the time scale of the tidal pulse is so much shorter, and is brief compared with the generation times of the higher biota.

Distinctions between aquatic and terrestrial organisms and processes have proved useful in studies of rivers and lakes with well-defined borders. The ecologist's view of floodplains, however, may vary according to the group of organisms being studied. Many of the organisms colonizing floodplains have developed adaptations that enable them to survive during an adverse period of drought or flood and even to benefit from it; thus neither a purely aquatic nor a wholly terrestrial view is appropriate.

Fisheries biologists tend to consider main channels and their floodplains as a single unit, because both are essential for the survival of fish stocks (Holčík and Bastl 1976; Welcomme 1979; Bayley 1980, 1981a, 1983). Conversely, studies of floodplains linked to African rivers or reservoirs show that they are also important for terrestrial game animals in adjacent nonflooded savannas, because the floodplains determine survival rates during the dry period (Sheppe and Osborne 1971; Davies 1985).

Were we to follow the arguments of hydrologists, all plant and animal material produced in a river–floodplain system would be autochthonous because it derives from riverine sediments and dissolved nutrients. Allochthonous would refer to the material introduced from outside the river–floodplain system. In limnological literature, however, the term autochthonous is applied to biota produced in the aquatic environment, and all terrestrial material is thereby classified as allochthonous. Oscillation between aquatic and terrestrial phases in floodplains makes the limnological differentiation of organic material according to its origin misleading. Similarly, the riparian zone, as understood in temperate areas, is difficult to define in a river–floodplain system. Consequently, we avoid unqualified references to these terms.

We have defined floodplain (ATTZ), river–floodplain system, and moving littoral, and explained why traditional limnological and hydrological paradigms are not appropriate from an ecologist's view. We now use examples to describe the effects of the flood pulse on biotic and abiotic components of the river–floodplain system.

Hydrology

The hydrological regime of rivers reflects the climate of its upstream catchment area. Low order streams have an irregular flood pattern with numerous peaks because they are strongly influenced by local precipitation. This influence generally diminishes with increasing size of the watershed and is almost imperceptible in the hydrograph of very large rivers.

The hydrological buffering capacity of a large catchment area results in a rather smooth and predictable flood curve. In mainly tropical or subtropical systems with large watersheds, the hydrograph reflects seasonality in precipitation, and typically shows only one pronounced flood peak per year. A few tropical rivers, e.g., the Zaire R., show two flood peaks due to two rainy seasons in their catchment areas. In temperate and cold climates, the impact of precipitation on the hydrograph is modified by the temperature regime. For example, minor flooding occurred in autumn in the Upper Mississippi R. prior to dam construction (Grubaugh and Anderson 1989a) because evapotranspiration rates decrease as temperature drops. Also, water accumulates as snow and ice in winter, which then contribute to the spring flood by melting.

Due to the size of large river basins, the effects of seasonal climatic changes may be felt downstream only after several weeks or even months. This time lag can be of ecological importance in downstream parts of large river systems. In the central Amazon the river is still rising at Manaus after the termination of the major rains; the flood peak follows the rainy season by 4–6 weeks. On the lower Mississippi R., cold water from melting snow in the head waters passes when the temperature in the backwaters of the floodplain is already much higher (Bryan et al. 1976; Holland et al. 1983).

The shape of the hydrograph depends not only on the discharge characteristics of the river, but also on valley slope, floodplain size, and vegetation. Although the Illinois R. has a mean discharge of only 627 $m^3 \cdot s^{-1}$ (Fitzgerald et al. 1986), it has protacted floods characteristics of a much larger river because it occupies a wide river valley carved by the ancestral Mississippi and Teays rivers. Because the valley has filled with alluvium, its gradient is very flat and the river drops only 1.6 $cm \cdot km^{-1}$.

At a given rate of discharge increase, the water level rises more slowly as the floodplain begins to fill. In larger floodplains the rate of rise is slower, the period of inundation increases, and more lentic habitats develop. As the water recedes, processes in the floodplain become less dependent on the river channel and more subject to local climatic events. During the terrestrial phase, the amount and distribution of local rains greatly affects the composition and productivity of plant communities as well as the life cycles of many animals. When local precipitation at low water is high, floodplains are forested, e.g., in the middle and upper Amazon, Zaire, and Mississippi rivers. Conversely, when local precipitation is low, savannas with gallery forest develop, e.g., in the floodplains of the lower Nile, Zambezi, and Volta rivers. Some lakes and swamps are isolated from the main channel for many months or even years. Their hydrological regimes are therefore independent of the main channel except during periods of high water.

Nutrients

According to hydrologists, a river's chemistry reflects its catchment area. This holistic view has been applied successfully to streams with respect to their nutrient budgets (Hynes 1975; Vannote et al. 1980). Nutrients can roughly be divided into inorganic and organic fractions; these in turn can be subdivided into gaseous compounds, dissolved solids, and particulate matter. The floodplain receives all classes of nutrients directly from the main channel, and its basic nutrient status would be expected to correspond to that of the river. Floodplains, however, tend to establish their own cycles since organisms and environmental conditions that influence the biogeochemical cycles differ considerably from those in the main channel. The effects of rain, runoff, groundwater, and input from floodplain tributaries may also be important.

The Inorganic Fraction

Gaseous Compounds

Gases such as CO_2, O_2, H_2S, CH_4, and N_2 are produced and/or consumed in the floodplain independently of processes in the main channel in systems with slow, regular flood pulses. Residence time of floodplain water and temperature modify concentrations. The lack of persistent thermal and chemical stratification in most Atchafalaya floodplain lakes is due to the short period of lentic conditions during warm weather (Bryan et al. 1974). In contrast, the water column becomes chemically stratified over large areas soon after entering the Amazon floodplain; the daily thermocline with a temperature difference of 1–3 °C is sufficient to inhibit circulation deeper than 2–6 m during periods of several weeks or even months. Large amounts of organic material under decomposition at high temperatures result in high rates of oxygen consumption and CO_2 release near the bottom. Hypoxic, or even anoxic conditions accompanied by H_2S and CH_4 production, are often found at a few metres depth (Schmidt 1973a; Melack and Fisher 1983; Junk et al. 1983).

In addition to nitrogen input from the river, high nitrogen fluxes to and from the atmosphere occur. These fluxes are related to oxygen levels and to organisms in water and soils, both of which change drastically between flood and dry periods. Denitrification in wetlands is well documented (Kemp and Day 1984) and has even been used in the treatment of wastewater (Dierberg and Breszonic 1984). Various nitrogen-fixing organisms, e.g., cyanophytes and bacteria, that are often associated with higher plants such as Leguminosae counteract denitrification by fixing atmospheric nitrogen (Heller 1969; Richey et al. 1985). Despite the high potential for denitrification, Brinson et al. (1980) consider tupelo-cypress swamps to be nitrogen sinks due to high nitrogen levels in the litter.

Dissolved Solids

River water is the major source for dissolved inorganic compounds, including plant nutrients. Abiotic and biotic processes in the floodplain, however, may considerably alter the total amount and ionic composition of dissolved materials. Increased evaporation may raise salinity in backwaters above the levels found in the river, in particular in arid climatic zones. Biogenic modifications are reported from Amazonian floodplain lakes where ten to twentyfold increases in total salinity have been measured in small pools at low water (Furch et al. 1983). A major change in ionic composition, such as an increase in potassium, has been principally associated with leaching of decomposing aquatic and terrestrial macrophytes (Furch 1984a, 1984b; Furch et al. 1983).

Further changes in ionic composition result from dilution by local rains or by mixing with lateral inflows of surface and ground water from nonflooded areas. During low river stages in the Amazon, water seeping through floodplain sediments has an electric conductance up to 200 times that of the Amazon R. water, with high levels of iron and manganese (Irion and Junk, unpublished data).

Levels of dissolved nutrients are seldom limiting factors for primary production in the main channels of large rivers. In the floodplain, however, phosphorous and/or nitrogen often limit productivity, and inflowing river water replenishes the nutrient levels, as shown for phytoplankton production in Amazonian floodplain lakes (Fisher 1979). In lake and swamp habitats receiving minimal influence from the Atchafalaya R., heterotrophic phytoplankters (flagellated euglenophytes and pyrrophytes) predominated during low water levels in association with minimal inorganic nutrients (Bryan et al. 1976; Seger and Bryan 1981).

Little is known concerning the amount of dissolved inorganic compounds released from the floodplain into the main channel, and findings are contradictory for phosphorous (Yarbro 1983) and nitrogen (Brinson et al. 1983). Release and storage may be related to the flood cycle and to vegetation cover, and in temperate regions, to the growth cycle of the vegetation (Klopatek 1978; Brinson et al. 1980). Because large floodplains represent a mosaic of habitats with different physical and chemical conditions supporting diverse biotic communities, they may act either as a sink, or as a source with respect to each nutrient, depending on the circumstances.

Particulate Matter

Particulate inorganic matter in suspension is normally considered an unimportant source of plant nutrients in the river channel. Conversely, such particles hinder growth of phytoplankton and submersed aquatic macrophytes due to shading. In floodplains, however, they become a basic part of the nutrient pool available to primary producers in the dry phase and during part of the wet phase. Fertility of floodplains depends largely upon the quality of deposited sediments. Irion (1983) states that transport and deposition of sandy and kaolinitic material produce an infertile floodplain (e.g., Rio Negro in Brazil), whereas the montmorillonite and illite of the Amazon and Mississippi rivers result in high floodplain fertility. However, an impoverishment of some mobile elements (Fe, Mn, Zn) was detected in the upper 10 m-layer of Amazon sediments, which are only a few hundred years old (Irion et al., unpublished data). Conversely, weathering of the sediments, which is accelerated in tropical climates, adds dissolved inorganic materials.

The Organic Fraction

According to the RCC, aquatic animal communities of low-order streams depend mainly upon material from the nonflooded watershed. Medium-order streams have an increased instream production. Fauna of high-order rivers lacking floodplains depend mainly on organic material from upstream areas because primary production in the main channel is very low (Vannote et al. 1980).

Practically all litter must be processed by microorganisms if it is to become attractive to higher consumers. A considerable portion continues to be practically indigestible, such as fine particulate organic material in the Amazon main channel (Hedges et al. 1986). Ertel et al. (1986) reported that humic materials comprised 60 % of the dissolved organic carbon of the Amazon main channel; this carbon in turn made up about 50 % of the total organic carbon. The comparatively low BOD of the water from the main channel of the Amazon itself contrasts sharply with values in its floodplain (Junk, unpublished data).

Part of the organic carbon transported in the main channel passes on to the floodplain. This amount, however, is negligible in comparison with in situ production of organic material in the floodplains of rivers (Bayley 1989). Estimates of the productivity of the Amazon floodplain show that annual primary production is of the same order of magnitude as the total amount of carbon transported by the river to the Atlantic Ocean (Richey et al. 1980; Junk 1985a).

The direct impact of floodplains on the carbon budget of main channels is not well known. Some evidence suggests that floodplains can be a source for particulate and dissolved carbon (Chowdhury et al. 1982; Martins 1982; Junk 1985a; Furch and Junk 1985; Grubaugh and Anderson 1989b). Conversely, retention mechanisms, such as settling of particulates, uptake by organisms, and retention of most macrophytes by stranding or trapping during falling water (Junk 1980) contribute to the recycling of most carbon in the floodplain and strongly reduce leakage to the river channel. Carbon export from floodplains also depends on hydroperiod, flushing rate, and in temperate regions, on the growth cycle of floodplain vegetation. Data from floodplains are limited, but Odum and de la Cruz (1967) estimated that the rate of export of organic material from a Georgia tidal marsh was directly proportional to volumetric flow rates.

Gosslink et al. (1981) assumed that flooding during winter and spring provides more detritus to main channels than during summer in temperate regions. In the tropics, consistently high temperatures favor high production and rapid processing of organic material throughout the year.

Biota in the River Channel

The channel is well defined in large, pristine rivers, and is delineated from the floodplains by natural levées and/or a marked increase in water velocity. In rivers modified by navigation dams, such as the Mississippi, broad, slow-flowing main channel borders are found on either side of the narrow main channel, which is defined by the thalweg (Fremling et al. 1989). These borders, which constitute a developing floodplain, are discussed separately below; however, the main channels of modified rivers have much in common with those in more pristine systems.

Plants

Great water depth, high suspensoid load, considerable turbulence, and strong current make the main channel unfavorable for primary production. Aquatic macrophytes and periphyton normally colonize shores and, in some transparent tropical rivers, rocky substrates (Podostemaceae). In slow-flowing tropical and subtropical rivers floating macrophytes may become important. Phytopotamoplankton density increases with stream order, transparency, and decreasing current velocity, but absolute values are low (e.g., Berner 1951). In most large rivers, physical factors, in particular light, rather than mineral nutrients limit primary production (Fisher 1979). Average primary production per unit area in the main stems of large turbid river systems such as the Amazon, Mekong, Ganges, and Mississippi can be only a small fraction of that in their floodplains.

The extent to which floodplain water bodies contribute to populations of potamoplankton and floating macrophytes in large rivers is unknown. The considerable increase of potamoplankton downstream of reservoirs, e.g., in the Nile (Brook and Rzóska 1954; Talling and Rzóska 1967; Hammerton 1976) and the increase of floating macrophytes in the Amazon main channel at rising and high water (Junk 1970) are due to high production of these plants in associated lentic habitats.

Invertebrates

Little information is available about colonization by animals of the bottoms of large rivers. The bed loads of large rivers in alluvial plains, e.g., the Mississippi, are sandy (Schumm 1977). Large river channels mostly consist of a monotonous sequence of slowly moving sand dunes unsuitable for benthic organisms. The Amazon R., for example, transports its bed load of coarse sand as dunes 6–8 m high (Sioli 1984).

High suspensoid loads hinder benthic and epizoic animals (Hynes 1970). Junk (1973) found a decrease in number and biomass of principally filter-feeding perizoon in floating macrophyte vegetation as amounts of inorganic suspensoids increased.

Although some invertebrates can live in the dominant sandy substrates of main channels (e.g., the chironomids *Gillotia*, *Cyphonella*, *Robackia*, and *Saetheria* [Coffman and Ferrington 1984]), densities are low. Berner (1951) and Morris et al. (1968) indicated average fresh invertebrate biomasses in the main channel of only 0.001 $g{\cdot}m^{-2}$ and 0.007–0.048 $g{\cdot}m^{-2}$, respectively, for the Missouri R., and attributed these low values to shifting substrates, siltation, fluctuating water levels, swift current, and absence of aquatic vegetation. In the Atchafalaya distributary, which receives 80 % of the Mississippi R. discharge, Bryan et al. (1976) reported a mean quantity of 327 benthic individuals per m^2 in riverine habitats compared with densities up to ten times greater in floodplain habitats.

Logs and rocks provide stable substrates for organisms in a channel environment that is otherwise dominated by shifting alluvium. Over 10^6 logs were pulled from channels in the lower 1600 km of the Mississippi during a 5-year period (Harmon et al. 1986). The average fresh animal biomass colonizing logs in the Kaskaskia R., Illinois, varied between 0.57 and 1.65 $g{\cdot}m^{-2}$ (Nilsen and Larimore 1973). Nord and Schmulbach (1973) reported a range of 0.2–3.2 $g \cdot m^{-2}$ dry weight in the Missouri R. Assuming an average surface area per log of 5 m^2, a dry biomass density of 2 $g \cdot m^{-2}$ of log, and an average width of the lower Mississippi channel of 900 m, the overall biomass density of this fauna would be only 0.007 $g \cdot m^{-2}$.

Vertebrates

Vertebrates, particularly fish, are important consumers in the main channel. In subtropical and tropical rivers, freshwater dolphins, capybaras, manatee, hippos, turtles, and crocodiles may contribute considerably to the main channel biomass. White whales and seals occur in arctic rivers; beavers, muskrats, and otters in temperate rivers; and waterfowl and shorebirds in both. However, few higher animals have adapted to utilize main channel habitats exclusively. Those that do tend to be predators whose prey depends largely on production in floodplain habitats, such as large, piscivorous catfishes (Goulding 1981), to some extent river dolphins (Ferreira da Silva 1983), and fish that consume aquatic invertebrates (Lundberg et al. 1987). In the main channels of the Mississippi and Missouri rivers, pallid sturgeon (*Scaphirynchus albus*), blue sucker (*Cycleptus elongatus*), blue catfish (*Ictalurus furcatus*), and several chubs (*Hybopsis* spp.) feed largely on invertebrates, and, with respect to large pallid sturgeons and blue catfish, on fish (Pflieger and Grace 1987).

Most vertebrates use the main channel temporarily as migration routes, for spawning, as refuge during droughts or freeze-up, or for hibernation. Tropical rivers are famous for large-scale migrations of fish for dispersal and/or spawning in the main channel or floodplain, that result in large biomass densities in the main channel during falling or low-water periods (Godoy 1967; Bonetto et al. 1969a; Bayley 1973; Ribeiro 1983). Large channel catfish (*Ictalurus punctatus*), flathead catfish (*Pylodictis olivaris*), and freshwater drum (*Aplodinotus grunniens*) use drop-offs, scour holes or obstructions in or along the main channel of the Upper Mississippi R. for a winter refuge (Hawkinson and Grunwald 1979).

Except for limited amounts of potamoplankton, benthos, and predators, the biota of the main channel concentrate close to the river shoreline, to islands, or in the main channel border areas described below, areas where habitat diversity increases and food supply improves (edge effect). Therefore the "bank coefficient" (Sedell et al. 1989) is an index of the productivity potential of a river channel in the absence of a floodplain. Conversely, when a regularly inundated floodplain is present, most of the vertebrates found in the main channel depend to a great extent directly or indirectly on primary production in the laterally linked floodplain habitats.

Biota in the Floodplains

Flood Pulsing and Life Cycles

Life cycles of biota utilizing floodplain habitats are related to the flood pulse in terms of its annual timing, duration, and the rate of rise and fall. Timing is important in temperate rivers where seasonal temperature and light cycles also regulate productivity.

Because the ATTZ has pronounced aquatic and terrestrial phases, there are strong selective pressures on aquatic organisms to colonize it at rising or high water because of the feeding opportunities (Bonetto et al. 1969b; Welcomme 1979; Bayley 1983, 1988). Conversely, terrestrial organisms that occupy nonflooded habitats along the floodplain borders are adapted to exploit the ATTZ at low water levels (Sheppe and Osborne 1971; Fredrickson 1979; Davies 1985).

In low-order streams, the level of adaptation to flooding is rather low. For many organisms, unpredictable floods correspond to catastrophic events that periodically "reset" the physical and biotic environment (Cummins 1977; Fisher 1983). Obligate aquatic organisms concentrate mostly in the main channel because flood periods are too short and irregular to develop profitable strategies for occupying the ATTZ.

The predictable and prolonged flood pulse typical of large rivers favors the development of anatomical, morphological, physiological, and/or ethological adaptations of terrestrial and aquatic organisms in order to colonize the ATTZ as shown by Adis (1979) and Irmler (1981) for Amazonian terrestrial invertebrates and by Uetz et al. (1979) and Wharton et al. (1981) for N. American floodplains.

In the humid tropics, regular flooding and drying of floodplains provoke a pronounced seasonality in an otherwise unseasonal environment. Many Amazonian floodplain trees show distinct annual growth rings, because inundation causes a "physiological winter" through oxygen stress (Worbes 1985, 1986). Seed production is timed with the flood for dispersal by water or by fish (Gottsberger 1978; Goulding 1980). Terrestrial arthropods from central Amazonian floodplain forests show a defined reproduction period (Adis and Mahnert 1986; Irmler 1986) but are polyvoltine in neighboring dryland forests (Adis and Sturm 1989). The flood cycle has been hypothesized as the driving force behind species selection ("taxon pulse", Erwin and Adis 1982) and the acquisition of an annual seasonality that enabled tropical insects to colonize temperate zones (Paarmann et al. 1982; Adis et al. 1986). The regular pulsing of large rivers may have been as important for the development of biorhythms in the tropics as was the pulsing of the light/temperature regime in temperate regions or the change between dry and wet periods in the arid and semiarid tropics.

Because many vertebrates living in the main channel depend on the floodplain for food supply, spawning, and shelter, they have developed strategies to utilize periodically available habitats. High mobility is required, as witnessed by the extensive migrations referred to earlier. Such strictly aquatic animals as fish and manatees depend on the flood cycle of the river, which controls access to the floodplain. Others less strictly aquatic, such as hippos, beavers, or capybaras, make feeding trips out of the water.

The importance of lateral migration of animals between the floodplain and main channel of large river systems has been underestimated because modern civilization has substantially modified the hydrograph and separated floodplains from main channels. These modifications dominate large temperate river systems. The biologist's typical view of fish in temperate rivers has been that they complete their life cycles within the river channel. Indeed, fish have no alternative in sections of some highly altered systems such as major stretches of the Mississippi R. Their persistence in these areas attests to their great plasticity in coping with habitat change.

Fishes that depend on seasonal colonization of floodplain habitats dominate the fisheries, the biomass, and the production in river–floodplain systems (Bonetto et al. 1969a; Welcomme 1979; Bayley 1981a; Goulding 1981; Bayley 1983; Littlejohn et al. 1985). Spawning of many species occurs at the beginning or during some period of the rising flood, resulting in timely colonization of the floodplains for feeding and shelter (Bayley 1983, 1988; Holland et al. 1983; Welcomme 1985). Conversely, when the water recedes, fish find refuge in main channels, in residual floodplain water bodies, or in permanent tributaries (Welcomme 1979).

Adults of many species show seasonality in food uptake related to flood cycles, as shown for the Rupununi R. by Lowe-McConnell (1964) and for the large rivers of the Amazon basin by Goulding (1980, 1981) and Ribeiro (1983). Periods of fasting coincide with low or falling water levels and are associated with decreases in seasonal fat content in many adult fish (Junk 1985b). Studies of diets at rising and high water show that many species directly use pollen, fruits, seeds, and the small portion of terrestrial insects that drop into the water from the canopy of the forest (Goulding 1980).

Detritus plays a major part in the food webs in floodplains (Welcomme 1985). Fish are major detritivores in the tropics. For example, fine particulate organic matter (FPOM) is consumed directly by the highly specialized Prochilodontidae and Curimatidae in South America, and by Citharinidae and *Labeo* species in Africa (Bowen 1984; PBB, pers. obs.). Coarse particulate organic matter (CPOM) features in the diet of many omnivores in the Amazon (Almeida 1980; Santos 1981).

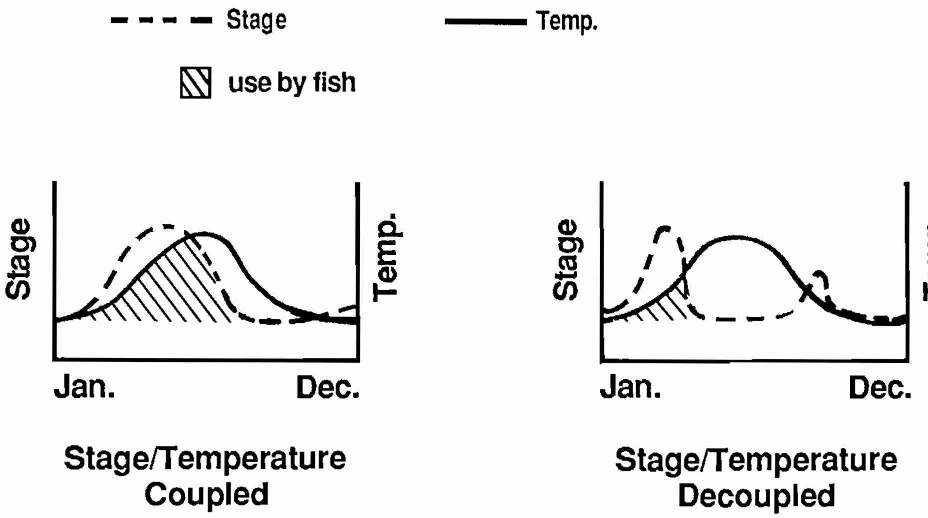
FPOM is also an important feature of the gut contents of large catostomids and *Dorosoma* in large N. American rivers, but its nutritional importance has only recently been indicated (Ahlgren 1988). Most of the commercially important fishes are bottom feeders utilizing macroinvertebrates, which in turn ingest detritus (Fremling et al. 1989).

The importance of remnant floodplain areas in the Mississippi and its tributaries was indicated by Risotto and Turner (1985), who found that 55 % of the variation in average fish catch was explained by bottomland hardwood area (as a proxy to floodplain area), fishing effort, and latitude. Because some bottomland forest is now cut off by manmade levees and not all floodplains are forested, the relationship might be improved with direct measurements of the active floodplain areas.

Adaptations to survive hypoxic conditions favor the colonization of periodically stagnant waters typical of many floodplains. Air breathing and other adaptations to low oxygen concentrations are frequently found in neotropical fishes (Carter and Beadle 1931; Kramer et al. 1978; Junk et al. 1983), other tropical floodplain rivers (Welcomme 1979), and in fish of the Mississippi drainage (e.g., gars, *Lepisosteus* spp. and bowfin, *Amia calva*; see also Marvin and Heath 1968).

In the temperate Upper Mississippi R. floods can reduce the overwinter survival of young-of-the-year freshwater drum (*Aplodinotus grunniens*) by the influx of channel water at 0°C into backwater thermal refuges where the temperature is 4°C (Bodensteiner and Sheehan, in press). The winter biology of fishes in large North American rivers has been little studied, and the recruitment of other species may be strongly affected by winter temperatures and flood patterns. From spring through summer, the timing and duration of the flood is critical to species which gain access to the ATTZ and permanent backwaters for feeding and spawning. Ideal conditions for spring spawners occur during years in which the flood and temperature rise are coupled; conversely, recruitment is poor if the flood retreats too soon during the warm growing season (Fig. 1). Finger and Stewart (1987) found that the timing and duration of flooding controlled the year-class dominance of spring- versus summer-spawners in Missouri floodplain forests.

In polar, sub-arctic, and taiga rivers the timing of the flood is predictable because of massive snow melt in the spring. However, the flood is accompanied by ice that scours the floodplains and subsequently recedes rapidly,



Stage/Temperature Coupled

Stage/Temperature Decoupled

FIG. 1. Schematic of combinations of river stage and water temperature in temperate river–floodplain systems (see text).

creating an inhospitable environment for fishes (Roy 1989). The severe springtime conditions may explain why fish in high latitudes avoid the flood by spawning in the fall (R.A. Ryder, personal communication).

Tree growth is mainly retarded by floods because the rhizosphere becomes deoxygenated (Huffman 1980; Huffman et al. 1981). Gosselink et al. (1981) postulated that floods during winter or spring have a positive effect on the floodplain forest because they distribute nutrients and water to the soil before plant growth commences. Data on flood tolerance of tree species often appear to be contradictory because the timing of floods relative to growth and resting periods is not stated (Dister 1980).

The Mississippi R. is a major migratory flyway for waterfowl, shorebirds, gulls, and eagles. The dabbling ducks (mallard, pintails, greenwing and bluewing teal, black duck) utilize mast in floodplain forests, waste grain in adjacent harvested fields, and invertebrates associated with macrophytes in shallow water bodies, as well as the seeds, tubers, and plant leaves in the floodplain (Bellrose 1941). The diving ducks (canvasback, lesser scaup) utilize submerged macrophytes and macroinvertebrates that grow in deeper water (Thompson 1973). Aquatic and moist-soil vegetation in the Illinois and Upper Mississippi floodplains requires a period of shallow, stable water levels during the summer growing season (Bellrose et al. 1979). The summer's primary production is made more accessible to migratory waterfowl by the autumn rise in water levels. If an autumn flood does not occur, managers of refuges and duck clubs create one by pumping water from the river into the floodplain. They also pump water out of the same impoundments if the flood is too slow to retreat in the summer, so they can sow millet or allow native plants to grow (Bellrose et al. 1979).

Flood Pulsing and Plant Community Structure

Under given climatic conditions, plant communities become established in the ATTZ of large rivers according to the flood regime. Every place in this zone can be considered a point on a gradient reflecting the degree of annual flooding. Every plant has its optimum position on this gradient. The optimum, however, can be modified by such factors as stability, structure, and fertility of the substrate, groundwater level, and biogenic processes (e.g., accumulation of organic material, nitrogen fixation, and interspecific competition) (Lindsey et al. 1961; Bedinger 1979; Burgess et al. 1973; Johnson and Bell 1976; Bell 1980; Dister 1980, 1983; Gosselink et al. 1981; McKnight et al. 1981). Distributions of animals are also affected by this gradient in spite of their mobility (Wharton et al. 1981; Larson et al. 1981).

Basic changes in plant community structure occur mainly through a shift of the gradient, such as a rise of the floodplain surface due to additional inorganic or organic sediment deposition (allogenic or autogenic succession), a lowering by erosion, or a change in the hydrograph due to climatic change, tectonic movement, or human influence such as the construction of a dam or lateral dikes.

Plant communities, however, are characterized by smaller changes. There is strong pressure on communities to proceed to a later successional stage when the period of the flood pulse is reduced. The shape of the pulse often varies within large limits, thereby causing communities to respond. Annual plants react to annual differences whereas forest communities are affected by extreme annual floods, droughts, or even periods of successive years of extreme flood events that may occur every 10, 20, or 100 years. Establishment of tree seedlings in low-lying areas requires a period of exceptionally low water for several years, as Demaree (1932) found for *Taxodium distichum*. Aquatic communities tend to fill up periodically isolated water bodies with organic debris, thereby causing autogenic succession to marsh and swamp vegetation when the flood pulse fails. This process has been estimated to require about 200 years in the temperate Rhône R. (Amoros et al. 1986). Extreme floods clean these water bodies and "reset" communities to earlier successional stages. Resets can be especially severe when floods occur during the ice season in temperate rivers because trees and channels can be scoured by wind- or water-driven ice (Sigafoos 1964). Consequently, the observed community structure in floodplains is a result of short-, medium-, and/or long-term effects of the flood pulse. Shelford (1954) estimated that about 600 years were required to develop the late subclimax tulip-deer-oak communities on the lower Mississippi R. Most communities receiving the full amplitude of the flood pulse can be viewed as being in a dynamic equilibrium at an early successional level (pulse-stability, *sensu* Odum 1959; see also Margalef 1968).

Flood Pulsing and Production

Primary and secondary production in the river–floodplain system is the sum of production during terrestrial and aquatic phases. As indicated previously, the basic fertility of the floodplain depends on the nutrient status of the water and on the sediments deriving from the river. This fertility, however, may be modified by tributaries and by runoff from the local catchment area of the floodplain. Length, amplitude, frequency, timing, and predictability of the flood pulse determine occurrences, life cycles, and abundances of primary and secondary producers and decomposers, abundances which affect the level of exploitation and regeneration of the nutrient pool as well as its supply.

Gosselink and Turner (1978) proposed a classification of wetland systems according to a hydrodynamic energy gradient. They suggested that a positive relationship existed between productivity and water flow. Their theory may be valid within limits in a river–floodplain system; however, short-duration pulsing can flush out considerable organic matter and nutrients into the main channel (or into the estuary from a salt marsh as shown by Teal [1962]) and limit in situ productive processes and access by aquatic animals. In such systems, the aquatic biologist studying production is concerned with how the ATTZ benefits the river or the permanent lentic areas in the floodplain. Conversely, slow inundation of the same floodplain allows sufficient time for in situ processes along the moving littoral (Fig. 2), which traverses the ATTZ with each pulse. Aquatic and terrestrial biologists studying production in river–floodplain systems with slow pulsing should be concerned with how the river benefits the floodplain.

The flooding phase of the moving littoral (Fig. 2) finds its closest parallel to a reservoir in the process of being flooded (Wood 1951), with mineralized products from any preceding aquatic cycle and the current terrestrial one being

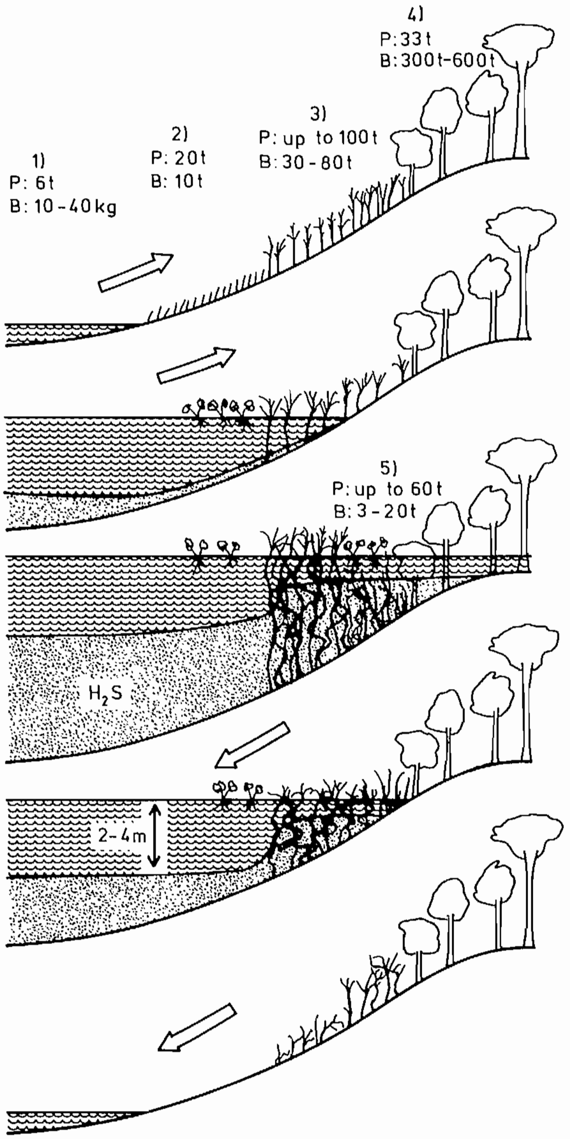


FIG. 2. The moving littoral in the transition zone (ATTZ) of a river-floodplain system in the central Amazon, with estimates of annual production (P) and biomass (B). Estimates are as dry weight per hectare. The H_2S zone has no dissolved O_2. The indicated zones are as follows: (1) Phytoplankton C14 (Schmidt 1973b), (2) annual terrestrial plants, (3) perennial grasses, (4) floodplain (várzea) forest, and (5) emergent macrophytes (from Junk 1985c and unpubl. data). Periphyton are not included, but preliminary data of periphyton on macrophytes from T. R. Fisher (pers. comm.) indicate a total productivity in the floodplain of the same order as phytoplankton (Bayley 1989).

released into the water. The various sources of primary production have high values (Fig. 2) but varying production to biomass ratios. When integrated over areas appropriate for each season in the floodplain, phytoplankton contributed less than 6 % of the total carbon production in the central Amazon várzea floodplain (Junk 1985a; Bayley 1989).

Most carbon sources, including considerable detrital biomass, are important to some animals at some time (Welcomme 1979, 1985; Junk 1984), but their quantitative importance is unknown. Organic material produced in floodplains varies considerably with respect to consistency, protein content, digestibility, and availability, that result in large differences in decomposition time and in the types of organisms involved in decomposition processes. Phytoplankton and periphyton are easily decomposed in only a few hours or days. In the Amazon, aquatic and terrestrial herbaceous plants lose about 50 % of their weight after 2–3 weeks in water (Howard-Williams and Junk 1976). Tree leaves vary widely according to species; some are as quickly decomposed as herbaceous plants whereas others remain little modified throughout months and even years. Softwood plants are destroyed in a few years, whereas hardwood plants may remain little modified for years and even decades (Junk, unpublished data).

Strong evidence suggests that the change between terrestrial and aquatic phases accelerates the decomposition of organic material, as the circumstantial evidence of Wood (1951) indicated. Terrestrial arthropods play an important role in the decomposition of leaf litter and wood as shown for cockroaches by Irmler and Furch (1979) and for termites by C. Martius (pers. comm. to WJJ). Oxygenation of sediments during dry periods promotes processing of organic material; later, when reflooding occurs, plant nutrients are recycled into the water, thereby enhancing productivity. This effect, sometimes in combination with a crop plantation or fallow period for an entire year, has been utilized for many years in European fish culture. Wood (1951) proposed the management of water levels in impoundments by changing them seasonally to increase fish production. Lambou (1959) suggested that the processes described by Wood explain the high productivity of backwater lakes due to natural water fluctuations in the Mississippi floodplain. In the Amazon floodplain during the period of rising water, mean growth increments by weight of 12 common fish species were 60 % higher than during the remainder of the year (Bayley 1988).

Food supply in fertile floodplains during the flood phase can be so abundant that factors other than food may limit individual growth and population density of fish and other aquatic animals. Limitations during the flood phase include spawning success, lack of habitats with sufficient dissolved oxygen (Junk et al. 1983), and predation (Bayley 1983). Limitations at low water include higher levels of predation, a probable reduction in food supply, or even death by drought. Bayley (1988) found that growth of juveniles of 11 abundant fish species tested did not indicate a density-dependent relationship with potentially competing species guilds during the period of rising water. Only two out of eight species indicated density-dependency at $P < .05$ during the shorter falling-water period.

The preceding ideas have very little to do with traditional concepts of productive processes in rivers. The RCC predicts that lower reaches of river systems have low ratios of production to respiration (P/R) due to processing of material from upstream and reduced in situ production. Wissmar et al. (1981) noted that Amazon floodplain lakes have high respiration rates, and Melack and Fisher (1983) noted that carbon loss due to respiration exceeds the carbon contributed by phytoplankton. However, these are limnological perspectives that describe only part of the system. The evidence offered here for the lower reaches of the river–floodplain system indicates high in situ production and low importation of organic matter from upstream. Therefore, we predict high P/R ratios for large river–floodplain systems.

Flood Pulsing and Diversity of Habitats and Species

Sediments, which are deposited in the floodplain in well-defined geomorphological units, form bars, levees, swales, oxbows, backwaters, and side channels. Flowing water grades sediments according to grain size. The floodplain soils are stratified horizontally and vertically in a small scale pattern (Irion et al. 1983; Amoros et al. 1986), but the wind-induced transport of sediment may modify the water-induced sediment pattern.

The main river and its connecting channels represent the lotic part of the river–floodplain system; oxbow lakes, abandoned channels, and backwaters represent the lentic one. Both harbour sets of organisms which colonize the much more extensive, periodically flooded ATTZ and increase species numbers occurring in the floodplain.

Differences in the duration of flooding, in soil structure, and in vegetation result in small-scale habitats in the form of narrow, roughly parallel zones. This arrangement multiplies the edge effect far beyond that represented by the main channel and its islands. In addition to these topological edges, there are many physico-chemical edges in the form of sharp vertical and horizontal boundaries in oxygen, temperature, dissolved or suspended matter; in the main channel these are encountered only at confluences with tributaries or near the substrate. In the Amazon, oxygen levels in surface water may drop from about 5 mg$\cdot$L^{-1} in the main channel to 0.5 mg$\cdot$L^{-1} in the floodplain 50 m away (Junk et al. 1983).

Habitats shift horizontally and vertically according to the waterlevel (Fig. 2). In addition to this instability due to the moving littoral is another instability caused by sediment deposition and erosion by the river. Depending on the position of the river channel and its dynamics, habitats may be ephemeral or rather stable over decades or centuries. This affects such stationary organisms as trees.

Nonflooded areas inside and adjacent to the floodplain perimeter, as well as emergent vegetation or the floodplain forest canopy, can be termed terrestrial habitats. All of them harbour an abundance of plants and animals that colonize the ATTZ, increasing considerably the total number of plants and animals occurring in the system.

No attempt to explain the total diversity in all habitats has been made; however, studies on specific plant and animal groups show some tendencies and some apparent inconsistencies. Species diversity would be expected to be limited in aquatic and terrestrial taxa that are sedentary and experience the full impact of the physiological stress resulting from the change between the aquatic and terrestrial phase. Worbes (1983) showed that the central Amazon floodplain forest has a much lower plant species diversity than the nonflooded forest. Salo et al. (1986), however, state that high diversity in tree species characterizing the upper Amazon lowland forests occurs in existing and relict floodplains, but they did not present species numbers or diversity indices. They describe a mosaic of small habitats created by large-scale, continuous disturbance by lateral erosion and sedimentation from the river channel, with high diversity between habitats. They reason that the high diversity in the relatively short-lived habitats of the present floodplains was due to insufficient time to allow competitive exclusion, supporting Connell's (1978) intermediate disturbance hypothesis. In the former floodplain formations that are about 5 000–10 000 years old, habitats are very stable, and the high species diversity between habitats was attributed by them to allopatric speciation.

Diversity would be expected to increase with the ability of organisms to avoid the physiological stress in the ATTZ. High diversity in floodplains occurs in mobile groups, such as fish (Lowe-McConnell 1975; Welcomme 1985) and nonaquatic birds (Remsen and Parker 1983).

The drastic change between terrestrial and aquatic phases results in high seasonal losses for most plant and animal populations, but these losses tend to be recovered by quick growth, early maturity, high reproduction rates for *r*-strategy organisms (Pianka 1970), and fast dispersal. Many of the most persistent and productive tropical aquatic weeds (e.g., *Eichhornia crassipes, Salvinia auriculata, Ceratopteris pteridoides,* and *Alternanthera philoxeroides*) are endemic to neotropical river–floodplains. In floodplains they are periodically decimated during the dry phase, allowing coexistence of many plant species with similar habitat requirements. In hydrologically stable conditions, they become dominant due to their strong competitive ability. Conversely, many persistent weeds in agricultural crops dominate in the early successional stages of floodplain vegetation at low water due to their *r*-strategy traits and recurrent disturbance of the ATTZ by the flood pulse (Seidenschwarz 1986; WJJ, unpublished data).

Many plants and animals show an impressive resilience with respect to short-term catastrophic events; an example is the rapid response of fishes following extreme drought, overfishing, or poisoning. Due to their highly effective reproduction strategies and to their mobility which allows access to dispersed low-water refuges, fish recover quickly when the flood pulse returns (Welcomme 1979). An *r*-strategy is effective only when sufficient nutrient and food resources are available to fully utilize the growth potential. Floodplains of extremely low nutrient status may therefore favor *K*-selection (Pianka 1970), such as Magalhães and Walker (1989) have indicated for Amazonian freshwater shrimps.

If we consider the total number of species in a river–floodplain system, circumstantial evidence suggests that a physical factor, the flood pulse, produces and maintains a highly diverse and dynamic habitat structure, thereby allowing a high species diversity despite stresses in the ATTZ. This is consistent with the intermediate disturbance hypothesis of Connell (1978) and parallels the observations of Statzner and Higler (1986) and Statzner (1987) who noted that physical factors (stream hydraulics) affected zonation patterns of benthic invertebrates, and that longitudinal zones of transition were associated with higher species richness.

Man-Made River-Floodplains

Dams have altered the hydrology and created artificial sedimentation basins covering thousands of square kilometres in rivers worldwide. Dam construction continues. For example, about 100 large reservoirs totalling 100 000 km^2 are projected to utilize the hydroelectric potential of Amazon R. tributaries (Junk and Melo 1987).

The hydrological changes often remove the flood pulse from floodplains downstream and sometimes permanently inundate floodplains upstream.

In the longer term, sedimentation and the modified flood pulse produce man-made river–floodplains. The 26 mainstem navigation dams on the Upper Mississippi R. downstream from Minneapolis, Minnesota, divide the river into reaches where the entire floodplain width immediately upstream of the dam is currently inundated, but where sedimentation is creating shallows that will become levées, side channels, or backwaters, and eventually floodplains (Fig. 3A to H). Of course, former floodplains now behind manmade levées will remain isolated from the river, assuming no long-term changes in flood stages or flood protection policy. The new floodplains upstream from some of these dams will experience the full amplitude of the flood cycle because the dams maintain water depths for navigation only during low flows but have little effect on flood levels. Indeed, the gates are raised completely out of the water and the relatively low earthen weirs that connect the locks and gates to the bluffs are overtopped during floods. The extent to which these developing floodplains contribute to secondary production, fish yield, and waterfowl utilization should be measurable during the next 50 years, assuming that other factors (e.g., pollution) remain constant or are taken into account. Thus the flood pulse concept can be investigated by measuring changes in one system through time since the navigation dam construction.

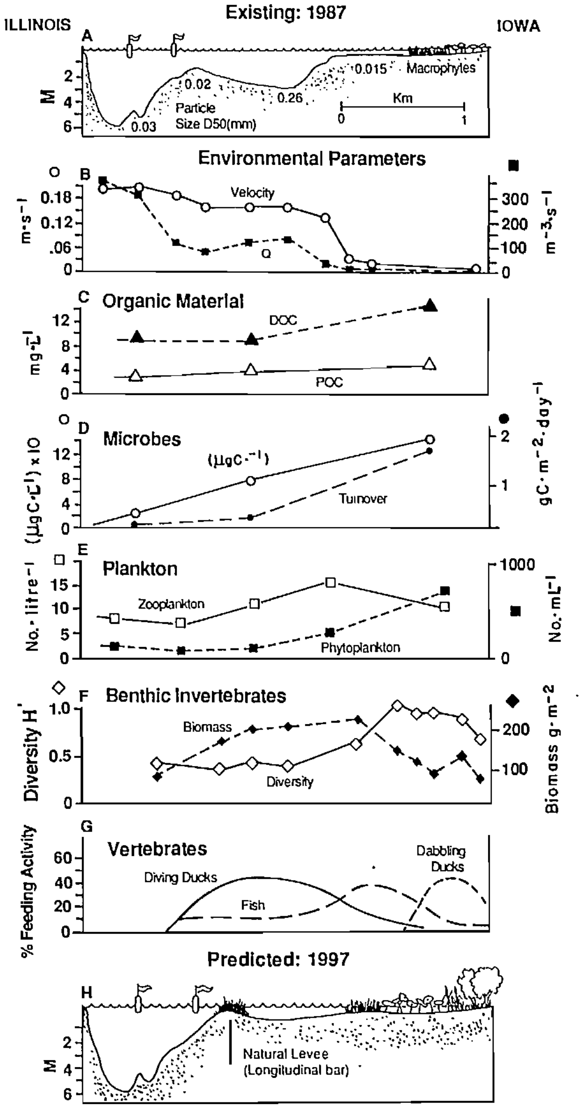


Fig. 3. A section of lower Keokuk Pool on the Upper Mississippi (A-G) with a projection of the stabilized system by the end of the century (H) (unpublished data from R. V. Anderson, R. E. Sparks, J. W. Grubaugh, K. S. Lubinski, and R. W. Gorden).

Even now, in an intermediate stage of succession in the Mississippi pools, the channel borders, not the main channel, are centers of production. Concentrations of particulate and dissolved organic carbon, plankton, and microbes are higher closer to the fringing plant beds and diminish toward the channel (Fig. 3C, E, and D). The greatest biomass of benthic macroinvertebrates are the burrowing filterers and collectors (mayflies of the genus *Hexagenia* and sphaeriid clams, *Musculium* and *Sphaerium*), which occur in beds just offshore of the macrophytes (Fig. 3F). These invertebrates apparently did not appear in high densities (up to 100 000 clams•m^{-2}) in the oldest pooled reach of the Mississippi R., the Keokuk Pool, until the 1960's (Gale 1969; Sandusky et al. 1979), when sedimentation raised the channel border bottom to the 1-m euphotic zone, thereby triggering autochthonous production by macrophytes. Diving ducks, which feed on concentrations of these invertebrates, only began using this pool in substantial numbers in the mid 1960's (Mills et al. 1966; Thompson 1973; F.C. Bellrose, pers. comm.). If phytoplankton or upstream sources had fueled the clams and mayflies, dense populations of these invertebrates should have been present in Keokuk Pool (but evidently were not) when Ellis (1931a, 1931b) made his biological surveys 18 years after the dam was closed, which was sufficient time for the accumulation of substrate suitable for burrowers. Organic matter was not being trapped behind upstream dams before it could enter the pool because these dams were not constructed until the late 1930's and early 1940's. The historical evidence from the Upper Mississippi R. thus supports the idea that a high level of secondary production requires a nearby center of primary production, rather than long-distance transport of organic matter from upstream sources via the main channel.

Conclusions

From a hydrological aspect, floodplains are part of the drainage system of rivers and are periodically affected by transport of water and dissolved and particulate material. From an ecological point of view, they represent transition zones (ATTZ) that alternate between aquatic and terrestrial states and link river channels with permanent lentic bodies and permanently dry land. Most large river systems have geomorphological settings that produce floodplains that are large relative to the lotic surface area (Welcomme 1985), and, in unmodified watersheds, produce a pulse of long duration that results in extensive but temporary lentic areas covering the ATTZ. Conversely, flood pulses of short duration, which are typical of low-order streams or of some modified systems, are associated with ATTZ's that are frequently covered by flowing water for short periods.

The flood pulse is the driving force for river–floodplain systems and maintains them in dynamic equilibrium. The system responds to the rate of rise and fall and to the amplitude, duration, frequency, and regularity of the pulses. Unpredictable pulses generally impede the adaptation of organisms and are counterproductive for many of them. Conversely, a regular pulse allows organisms to develop adaptations and strategies for efficient utilization of habitats and resources within the ATTZ, rather than depend solely on permanent water bodies or permanent terrestrial habitats. In temperate regions, the light and/or temperature regime may modify the biological effects of the pulse; timing of the pulse becomes important. In polar, sub-arctic, and taiga rivers where ice scouring occurs, the contribution to productivity from the ATTZ is not realized. In semiarid regions, local precipitation has a strong influence on the floodplain biota during the dry phase.

A variety of physical structures in combination with the flood pulse results in great habitat diversity. This diversity is coupled with the dynamic effect of the moving littoral, which extends the edge effect of the littoral over the entire ATTZ, thereby rendering channel banks bordering lotic zones insignificant by comparison. Organisms tend to invade the ATTZ from the terrestrial side also. Regular pulsing coupled with habitat diversity favors high diversity of aquatic and terrestrial plants and animals, despite considerable stress that results from the change between terrestrial and aquatic phases.

Aquatic and terrestrial productivity of river–floodplain systems depend mainly on the nutrient status of the water and sediments, on the climate, and on the flood pulse. Cycles specific to the floodplain, however, are decoupled to some extent from the nutrient status of the main channel. The moving littoral prevents permanent stagnation, thereby allowing the rapid recycling of organic matter and nutrients and resulting in a productivity that we predict to be greater than if the ATTZ were either permanently inundated or dry. Primary production associated with the ATTZ is much higher than that of permanent water bodies in unmodified systems and can often exceed that of permanent terrestrial habitats.

Transport of organic carbon from upstream catchment areas into the floodplain (spiralling) is of little importance to the productivity of the system. Conversely, primary and secondary production of the floodplains is essential to fauna in the main channels. A major component of energy transfer between floodplains and main channels is effected by animal migration, in particular of fish that also migrate upstream for considerable distances. Some bird species transfer nutrients from terrestrial areas or flooded mudflats, where they feed, to floodplain lakes, where they rest and defecate; other species do the reverse. The main function of the river channel in relation to plants and animals in the river–floodplain system is that of a migration route and dispersal system to access resources and refuges.

In conclusion, for those interested in the principal driving forces responsible for the structure, function, and evolutionary history of the biota in river–floodplain systems, we believe that the concept offered here will prove of heuristic rather than merely descriptive value. There is a fundamental dichotomy in the river–floodplain system: both continuous (e.g., the RCC) and batch processes occur. The latter, represented by the flood pulse concept, is dominant in systems with floodplains (ATTZs), in particular when the pulse is regular and of long duration. It is distinct because processes in floodplains do not depend on inefficient processing of organic matter upstream, although their inorganic nutrient pool may be replenished with periodic lateral inflows of water and sediments from the main channel. The pulse concept differs in that the position of the floodplain in the system relative to the river network is not a primary determinant of the processes that occur, although hydrological circumstances do not normally favor floodplain development in extreme upper reaches. However, examples do occur in upper reaches, such as the Pantanal of the Paraná system and the extensive Bolivian and Peruvian floodplains in the Amazon.

This concept implies an approach to studying the system different from the traditional limnological paradigms for either lotic or lentic systems. The space and time scales appropriate for understanding the mechanisms differ from those related to longitudinal processes in lotic channels. We hope that the flood pulse concept will help ecologists improve the design of studies and frame hypotheses that will lead more directly to a better understanding of river–floodplain systems. This is an urgent goal considering the modifications that continue to be proposed and that are sometimes put into practice in many tropical and temperate systems.

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References

(Addresses of personal communications follow references)

ADIS, J. 1979. Vergleichende ökologische Studien an der terrestrischen Arthropodenfauna zentralamerikanischer überschwemmungswälder. Ph.D. thesis, Ulm Univ., West Germany. 99 p.

ADIS, J., AND V. MAHNERT. 1986. On the natural history and ecology of Pseudoscorpiones (Arachnidae) from an Amazonian blackwater inundation forest. Amazoniana 9: 297–314.

ADIS, J., W. PAARMANN, AND T. L. ERWIN. 1986. On the natural history and ecology of small terrestrial ground beetles (Col.: Bembidiini: Tachyina: Polyderis) from an Amazonian blackwater inundation forest, p. 413–427. *In* P.J. Den Boer, M. L. Luff, D. Mossakowski, and F. Weber [ed.] Carabid beetles: their adaptations, dynamics and evolution, G. Fisher, Stuttgart, West Germany.

ADIS, J., AND H. STURM. 1989. Flood-resistance of eggs and life-cycle adaptation, a survival strategy of *Neomachilellus scandens* (Meinertellidae, Archaeognatha) in Central Amazonian inundation forest. Insect Sci. Appl. (In press)

Ahlgren, M. O. 1988. Diet selection and the seasonal contribution of detritus to the diet of the white sucker. Poster session of the 1988 American Fisheries Society Conference, Toronto, Canada.

Almeida, R. G. 1980. Aspectos taxonómicos e hábitos alimentares de três espécies de *Triportheus* (Pisces: Characoidei, Characidae), do lago do Castanho, Amazonas. M.S. thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil. 104 p.

Amoros, C., A. L. Roux, J. L. Reygrobellet, J. P. Bravard, and G. Pautou. 1986. A method for applied ecological studies of fluvial hydrosystems. Regulated Rivers 1: 17–36.

Andrews, C. W., and E. Lear. 1956. The biology of arctic char (*Salvelinus alpinus*) in northern Labrador. J. Fish. Res. Board Can. 13: 843–860.

Antipa, G. P. 1911. Fischerei und Flussregulierung. Allgem. Fischerei-Zeitung, München 16/17: 1–5.

1928. Die biologischen Grundlagen und der Mechanismus der Fischproduktion in den Gewässern der unteren Donau Academie Roumaine, Bull. de la Section Scientifique 11: 1–20.

Barmuta, L. A., and P. S. Lake. 1982. On the value of the river continuum concept. N. Z. J. Mar. Freshwater Res. 16: 227–231.

Bayley, P. B. 1973. Studies on the migratory characin *Prochilodus platensis* Holmberg 1889 (Pisces, Characoidei) in the Rio Pilcomayo, S. America. J. Fish Biol. 5: 25–40.

1980. The limits of limnological theory and approaches as applied to river–floodplain systems and their fish production, p. 739–746. *In* J.I. Furtado [ed.] Tropical ecology and development. Proceedings of the Vth International Symposium of Tropical Ecology. International Society of Tropical Ecology, Kuala Lumpur.

1981a. Fish yield from the Amazon in Brazil: comparisons with African river yields and management possibilities. Trans. Am. Fish. Soc. 110: 351–359.

1981b. Características de inundación en los rios y áreas de captación en la Amazonia Peruana: una interpretación basada en imagenes del 'LANDSAT' e informes de 'ONERN'. Inst. Mar. Peru(Callao) Inf. 81: 245–303.

1983. Central Amazon fish populations: biomass, production and some dynamic characteristics. Ph.D. thesis, Dalhousie Univ., Nova Scotia, Canada. 330 p.

1988. Factors affecting growth rates of young tropical fishes: seasonality and density-dependence. Env. Biol. Fishes 21:127–142.

1989. Aquatic environments in the Amazon Basin, with an analysis of carbon sources, fish production, and yield, p. 399-408. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Bedinger, M. S. 1979. Relation between forest species and flooding, p. 427–435. *In* P. E. Greeson, P. E. Clark, and J. E. Clark [ed.] Wetland functions and values: the state of our understanding. American Water Resources Association, Anthony Falls Hydraulic Laboratory, Minneapolis, MN.

Bell, D. T. 1980. Gradient trends in the streamside forest of central Illinois. Bull. Torrey Bot. Club 107: 172–180.

Bellrose, F. C. 1941. Duck food plants of the Illinois River valley. Ill. Nat. Hist. Surv. Bull. 21: 237–280.

Bellrose, F. C., F. L. Paveglio, Jr., and D. W. Steffeck. 1979. Waterfowl populations and the changing environment of the Illinois River valley. Ill. Nat. Hist. Surv. Bull. 32: 1–54.

Berner, L. M. 1951. Limnology of the lower Missouri River. Ecology 32: 1–12.

Bhowmik, N. G., and J. B. Stall. 1979. Hydraulic geometry and carrying capacity of floodplains. Univ. of Illinois Water Resources Center. Research Report 145 UI LU-WRC-79-0145, Champaign, IL. 147 p.

Bodensteiner, L. R., and R. J. Sheehan. 1989. Implications of backwater habitat management strategies to fish populations. Proceedings of the 44th Annual Meeting of the Upper Mississippi River Conservation Committee. 8–10 March 1988, Peoria, Il. (In press)

Bonetto, A. A., W. Dioni, and C. Pignalberi. 1969a. Limnological investigations on biotic communities in the Middle Parana River Valley. Int. Ver. Theor. Angew. Limnol. Verh. 17: 1035–1050.

Bonetto, A. A., E. Cordiviola de Yuan, C. Pignalberi, and O. Oliveros. 1969b. Ciclos hidrológicos del Rio Paraná y las poblaciones de peces contenidas en las cuencas temporarias de su valle de inundación. Physis (Buenos Aires) 29: 213–223.

Bowen, S. H. 1984. Detritivory in neotropical fish communities, p. 59–66. *In* T. Zaret [ed.] Evolutionary ecology of neotropical freshwater fishes. Dr W. Junk, The Hague, Netherlands.

Bravard, J. P. , C. Amoros, and G. Pautou. 1986. Impact of civil engineering works on the succession of communities in a fluvial system. Oikos 47: 92–111.

Brinson, M. M., H. D. Bradshaw, and J. B. Elkins, Jr. 1980. Litterfall, stemflow, and throughfall nutrient fluxes in an alluvial swamp forest. Ecology 61: 827–835.

Brinson, M. M., H. D. Bradshaw, and R. N. Homes. 1983. Significance of the floodplain sediments in nutrient exchange between a stream and its floodplain, p. 199–221. *In* T. D. Fontaine, and S. M. Bartell [ed.] Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, MI.

Brook, A. J., and J. Rzóska. 1954. The influence of the Gebel Aulyia Dam on the development of Nile plankton. J. Anim. Ecol. 23: 101–114.

Bryan, C. F., F. M. Truesdale, D. S. Sabins, and C. R. Demas. 1974. Annual report on a limnological survey of the Atchafalaya Basin. Louisiana Cooperative Fishery Research Unit, School of Forestry and Wildlife Management, Louisiana State Univ., 1974. 208 p.

Bryan, C. F., D. J. Demont, D. S. Sabins, and J. P. Newman, Jr. 1976. Annual report on a limnological survey of the Atchafalaya Basin. Louisiana Cooperative Fishery Research Unit, School of Forestry and Wildlife Management, Louisiana State Univ., 1976. 285 p.

Bryan, C. F., and D. S. Sabins. 1979. Management implications in water quality and fish standing stock information in the Atchafalaya River Basin, Louisiana, p. 293–316. *In* J. W. Day Jr., D. D. Culley Jr., R. E. Turner, and A. J. Mumphrey Jr. [ed.] Proceedings from the Third Coastal Marsh and Estuary Symposium, Louisiana State Univ., Division of Continuing Education, Baton Rouge, Louisiana.

Burgess, R. L., W. C. Johnson, and W. R. Keammerer. 1973. Vegetation of the Missouri River floodplain in North Dakota. North Dakota Water Resource Research Institute Report WI-221-018-07: 162 p.

Carter, G. S., and L. C. Beadle. 1931. The fauna of the swamps of the Paraguayan Chaco in relation to its environment. II. Respiratory adaptations in the fishes. J. Linn. Soc. Lond. (Zool.) 37: 327–368.

Chowdhury, M. J., S. Safiullah, S. M. Iqbal Ali, M. Mofizuddin, and S. E. Kabir. 1982. Carbon transport in the Ganges and the Brahmaputra: preliminary results. Mitt. Geol. Paläont. Inst. Univ. Hamburg, SCOPE/UNEP Sonderbd. 52: 457–468.

Coffman, W. P., and L. C. Ferrington, Jr. 1984. Chironomidae, p. 551–652. *In* R. W. Merrit, and K. W. Cummings [ed.] An introduction to the aquatic insects of North America. 2nd. Edition, Kendall/Hunt Publishing Co., Dubuque, IA.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Cummins, K. W. 1977. From headwater streams to rivers. Am. Biol. Teach. 39: 305–312.

Curry, R. R. 1972. Rivers — a geomorphic and chemical overview, p. 9–31. *In* R. T. Oglesby, C. A. Carlson, and J. A. McCan [ed.] River ecology and man. Academic Press, New York, NY.

DAVIES, B. R. 1985. The Zambezi river system, p. 225–267. *In* B. R. Davies, and K. F. Walker [ed.] The ecology of river systems. Dr W. Junk, The Hague, Netherlands.

DAVIES, B. R., AND K. F. WALKER. 1985. River systems as ecological units. An introduction to the ecology of river systems, p. 1–23. *In* B. R. Davies, and K. F. Walker [ed.] The ecology of river systems. Dr W. Junk, The Hague, Netherlands.

DEMAREE, D. 1932. Submerging experiment with *Taxodium*. Ecology 13: 258–262.

DIERBERG, F. E., AND P. L. BRESZONIC. 1984. The effect of wastewater on the surface water and ground water quality of cypress domes, p. 83–101. *In* K. C. Ewel, and H. T. Odum [ed.] Cypress swamps. Univ. of Florida Press, Gainesville, FL.

DISTER, E. 1980. Geobotanische Untersuchungen in der hessischen Rheinaue als Grundlage für die Naturschutzarbeit. Ph.D. thesis, Göttingen Univ., West Germany. 170 p.

1983. Zur Hochwassertoleranz von Auwaldbäumen an lehmigen Standorten. Verhandlungen der Gesellschaft für ökologie 11: 325–336.

ELLIS, M. M. 1931a. Some factors affecting the replacement of the commercial fresh-water mussels. Bureau of Fisheries Circular, U.S. Dep. of Commerce 7: 1–10.

1931b. A survey of conditions affecting fisheries in the Upper Mississippi River. Bureau of Fisheries Circular, U.S. Dep. of Commerce 5: 1–18.

ERTEL, J. R., J. I. HEDGES, A. H. DEVOL, J. E. RICHEY, AND M. N. G. RIBEIRO. 1986. Dissolved humic substances of the Amazon River system. Limnol. Oceanogr. 31: 739–754.

ERWIN, T. L., AND J. ADIS. 1982. Amazonian inundation forests, richness and taxon pulses, p. 358–371. *In* G. T. Prance [ed.] Biological diversification in the tropics. Proc. Fifth Int. Symp. Assoc. Trop. Biol. Columbia Univ. Press, New York, NY.

FERREIRA DA SILVA, V. M. 1983. Ecología alimentar dos dolfinhos da Amazônia. M.S. thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil. 110 p.

FINGER, T. R., AND E. M. STEWART. 1987. Response of fishes to flooding regime in lowland hardwood wetlands, p. 86–92. *In* W. J. Mathews and D. C. Heins [Ed.] Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, OK.

FISHER, S. G. 1983. Succession in streams, p. 7–27. *In* J. R. Barnes, and G. W. Minshall [ed.] Stream ecology: application and testing of general ecological theory. Plenum Press, N.Y.

FISHER, T. R. 1979. Plankton and primary production in aquatic systems of the central Amazon Basin. Comp. Biochem. Physiol. 62A: 31–38.

FITZGERALD, K. K., P. D. HAYES, T. E. RICHARDS, AND R. L. STAHL. 1986. Water resources data, Illinois, Water Year 1985. Vol. 2. Illinois River Basin. U.S. Geological Survey Water Data Report IL-85-2, USGS, Urbana, IL. 397 p.

FOERSTER, R. E. 1968. The sockeye salmon, *Oncorhynchus nerka*. Fish. Res. Board Canada Bull. 162: 422 p.

FREDERICKSON, L. H. 1979. Lowland hardwood wetlands: current status and habitat values for wildlife, p. 296–311. *In* P. E. Greeson, P. E. Clark, and J. E. Clark [ed.] Wetland functions and values: the state of our understanding. American Water Resources Association, Anthony Falls Hydraulic Laboratory, Minneapolis, MN.

FREMLING, C. R., J. L. RASMUSSEN, R. E. SPARKS, S. P. COBB, C. F. BRYAN, and T. O. CLAFLIN. 1989. Mississippi River fisheries: a case history, 309–351. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

FURCH, K. 1984a. Interanuelle Variation hydrochemischer Parameter auf der Ilha de Marchantaria. Biogeographica 19: 85–100.

1984b. Seasonal variations of the major cation content of the várzea-lake Lago Camaleão, middle Amazon, Brazil, in 1981 and 1982. Int. Ver. Theor. Angew. Limnol. Verh. 22: 1288–1293.

FURCH, K., AND W. J. JUNK. 1985. Dissolved carbon in a floodplain lake of the Amazon and in the river channel. Mitt. Geol. Paläont. Inst. Univ. Hamburg, SCOPE/UNEP Sonderbd. 58: 285–298.

FURCH, K., W. J. JUNK, J. DIETERICH, AND N. KOCHERT. 1983. Seasonal variation in the major cation (Na, K, Mg and Ca) content of the water of Lago Camaleão, an Amazonian floodplain lake near Manaus, Brazil. Amazonia 8: 75–89.

GALE, W. F. 1969. Bottom fauna of Pool 19, Mississippi River, with emphasis on the life history of the fingernail clam *Sphaerium transversum*. Ph.D. thesis, Iowa State Univ., Ames. 234 p.

GODOY, M. P. de. 1967. Dez anos de observações sôbre periodicidade migratoria de peixes do Rio Mogi Guassu. Rev. Brasil. Biol. 27: 1–12.

GOSSELINK, J. G., AND R. E. TURNER. 1978. The role of hydrology in freshwater wetland ecosystems, p. 63–78. *In* R. E. Good, D. F. Whigham, and R. L. Simpson [ed.] Freshwater wetlands: ecological processes and management potential. Academic Press, New York, NY.

GOSSELINK, J. G., S. E. BAYLEY, W. H. CONNER, AND R. E. TURNER. 1981. Ecological factors in the determination of riparian wetland boundaries, p. 197–219. *In* J. R. Clark and J. Benforado [ed.] Wetlands of bottomland hardwood forests. — Developments in agricultural and managed forest ecology 11, Elsevier Scientific Publishing Company, Amsterdam, Oxford, New York, NY.

GOTTSBERGER, G. 1978. Seed dispersal by fish in the inundated regions of Humaita, Amazonia. Biotropica 10: 170–183.

GOULDING, M. 1980. The fishes and the forest: explorations in Amazonia natural history. California Univ. Press, Berkeley. 280 p.

1981. Man and fisheries on an Amazon frontier. Dr. W. Junk, The Hague, Netherlands. 137 p.

GRAINGER, E. H. 1953. On the age, growth, migration, reproductive potential and feeding habits of the Arctic char (*Salvelinus alpinus*) of Frobisher Bay, Baffin Island. J. Fish. Res. Board Can. 10: 326–370.

GRUBAUGH, J. W., AND R. V. ANDERSON. 1989a. Long-term effects of navigation dams on a segment of the Upper Mississippi River. Regulated Rivers. (In press)

1989b. Seasonal fluxes and the influences of floodplain forest on organic matter dynamics in the Upper Mississippi River. Hydrobiologia. (In press)

HAMMERTON, D. 1976. The Blue Nile in the plains, p. 243–256. *In* J. Rzóska [ed.] The Nile, biology of an ancient river. Dr. W. Junk, The Hague, Netherlands.

HARMON, M. E., J. R. FRANKLIN, F. J. SWANSON, J. D. LATTIN, S. V. GREGORY, N. H. ANDERSON, S. P. CLINE, N. G. AUMEN, J. R. SEDELL, G. W. LIENKAEMPER, K. CROMACK Jr., AND K. W. CUMMINS. 1986. Ecology of course woody debris in temperate ecosystems. Adv. Ecol. Res. 15: 133–302.

HAWKINSON, B., AND G. GRUNWALD. 1979. Observations of a wintertime concentration of catfish in the Mississippi River. Fisheries Investigation Report No. 365, Minnesota Dep. of Natural Resources. 9 p.

HEDGES, J. I., W. A. CLARK, P. D. QUAY, J. E. RICHEY, A. H. DEVOL, AND U. M. SANTOS. 1986. Compositions and fluxes of particulate organic material in the Amazon river. Limnol. Oceanogr. 31: 717–738.

HELLER, H. 1969. Lebensbedingungen und Abfolge der Flussauevegetation in der Schweiz. Schweiz. Anst. Forstl. Versuchswes. Mitt. 45: 1–124.

Holčík, J., and I. Bastl. 1976. Ecological effects of water level fluctuation upon the fish populations in the Danube River floodplain in Czechoslovakia. Acta Sci. Natur. Acad. Scient. Bojemoslov. Brno 10: 1–46.

1977. Predicting fish yield in the Czechoslovakian section of the Danube River based on the hydrological regime. Int. Rev. Gesamten Hydrobiol. 62: 523–532.

Holland, L. E., C. F. Bryan, and J. P. Newman, Jr. 1983. Water quality and the rotifer population in the Atchafalaya River Basin. Hydrobiologia 98: 55–69.

Howard-Williams, C., and W. J. Junk. 1976. The decomposition of aquatic macrophytes in the floating meadows of a Central Amazonian várzea lake. Biogeographica 7: 115–123.

Huffman, R. T. 1980. The relation of flood timing and duration to variation in bottomland hardwood community structure in the Quachita River Basin of Southeastern Arkansas. U. S. Army Engineer Waterways Experiment Station Miscellaneous Paper E-80-4, Vicksburg, Mississippi: 22 p.

Huffman, R. T., and S. W. Forsythe. 1981. Bottomland hardwood forests and their relation to anaerobic soil conditions, p. 187–196. *In* J. R. Clark and J. Benforado [ed.] Wetlands of bottomland hardwood forests. — Developments in agricultural and managed forest ecology 11, Elsevier Scientific Publishing Company, Amsterdam, Oxford, New York, NY.

Hynes, H. B. N. 1970. The ecology of running waters. Liverpool Univ. Press, England. 555 p.

1975. The stream and its valley. Int. Ver. Theor. Angew. Limnol. Verh. 19: 1–15.

Irion, G. 1983. Tonmineralien in der Schwebfracht von Flüssen des Amazonasgebietes und von Papua Neuguinea. Zentralblatt für Geologie und Paläontologie, Stuttgart 1: 502–515.

Irion, G., J. Adis, W. J. Junk, and F. Wunderlich. 1983. Sedimentological studies of the "Ilha da Marchantaria" in the Solimões/Amazon River near Manaus. Amazoniana 8: 1–18.

Irmler, U. 1981. Überlebensstrategien von Tieren im saisonal überschwemmtem amazonischen überschwemmungswald. Zool. Anz. 206: 26–38.

1986. Temperature dependent generation cycle for the cicindelid beetle *Pentacomia egregia* Chaud. (Coleoptera, Carabidae, Cicindelidae) of the Amazon valley. Amazoniana 9: 431–439.

Irmler, U., and K. Furch. 1979. Production, energy and nutrient turnover of the cockroach *Epilampra irmleri* Rocha e Silva and Aguiar in a Central Amazonian inundation forest. Amazoniana 6: 497–520.

Johnson, F. L., and D. T. Bell. 1976. Plant biomass and net primary production along a flood-frequency gradient in the streamside forest. Castanea 41: 156–165.

Junk, W. J. 1970. Investigations on the ecology and production biology of the floating meadows (Paspalo-Echinochloetum) on the Middle Amazon, Part 1: the floating vegetation and its ecology. Amazoniana 2: 449–495.

1973. Investigations on the ecology and production biology of the floating meadows (Paspalo–Echinochloetum) on the Middle Amazon, Part 2: the aquatic fauna in the root zone of floating vegetation. Amazoniana 4: 9–102.

1980. Areas inundáveis — Um desafio para Limnología. Acta Amazonica 10: 775–795.

1984. Ecology of the várzea, floodplain of Amazonian whitewater rivers, p. 215–244. *In* H. Sioli [ed.] The Amazon (Monographiae biologicae, Vol 56). Dr. W. Junk, The Hague, Netherlands.

1985a. The Amazon floodplain — a sink or source for organic carbon?. Mitt. Geol. Paläont. Inst. Univ. Hamburg, SCOPE/UNEP Sonderbd. 58: 267–283.

1985b. Temporary fat storage, an adaptation of some fish species to the waterlevel fluctuations and related environmental changes of the Amazon system. Amazoniana 9: 315–351.

1985c. Aquatic plants of the Amazon system, p. 319–337. *In* B. R. Davies and K. F. Walker [ed.] The ecology of river systems. Dr W. Junk, The Hague, Netherlands.

Junk, W. J., and J. A. S. N. de Mello. 1987. Impactos ecológicos das represas hidroelétricas na bacía amazonica brasileira. p. 367–385. *In* G. Kohlhepp and A. Schrader [ed.] Homem e natureza na Amazônia. Tübinger Geographische Studien Vol. 95.

Junk, W. J., G. M. Soares, and F. M. Carvalho. 1983. Distribution of fish species in a lake of the Amazon river floodplain near Manaus (Lago Camaleão), with special reference to extreme oxygen conditions. Amazoniana 7: 397–431.

Junk, W. J., and R. L. Welcomme. 1989. Management of floodplains. *In* B. C. Patten [ed.] Wetlands and shallow continental water bodies, Vol. 1. SPB Academic Publishing, The Hague, Netherlands. (In press)

Kemp, G. P., and J. W. Day. 1984. Nutrient dynamics in a Louisiana swamp receiving agricultural runoff, p. 286–293. *In* K. C. Ewel and H. T. Odum [ed.] Cypress swamps. Univ. of Florida Press, Gainesville, FL.

Klopatek, J. M. 1978. Nutrient dynamics of freshwater riverine marshes and the role of emergent macrophytes, p. 195–216. *In* R. E. Good, D. F. Whigham, and R. L. Simpson [ed.] Freshwater wetlands. Ecological processes and management potential. Academic Press, New York, NY.

Kramer, D. L., C. C. Lindsey, G. E. E. Moodre, and E. D. Stevens. 1978. The fishes and the aquatic environment of the Central Amazon Basin, with particular reference to respiratory patterns. Can. J. Zool. 56: 717–729.

Lambou, V. W. 1959. Fish populations of backwater lakes in Louisiana. Trans. Am. Fish. Soc. 88: 7–15.

Larson, J. S., M. S. Bedinger, C. F. Bryan, S. Brown, R. T. Huffman, E. L. Miller, D. G. Rhodes, and B. A. Tuchet. 1981. Transition from wetlands to uplands in southeastern bottomland hardwood forests, p. 225–273. *In* J. R. Clark and J. Benforado [ed.] Wetlands of bottomland hardwood forests. — Developments in agricultural and managed forest ecology 11, Elsevier Scientific Publishing Company, Amsterdam, Oxford, New York.

Lindsey, A. A., R. D. Petty, D. K. Sterling, and W. van Asdall. 1961. Vegetation and environment along the Wabash and Tippecanoe Rivers. Ecol. Monogr. 31: 105–156.

Littlejohn, S., L. E. Holland, R. Jacobson, M. Huston, and T. Hornung. 1985. Habits and habitats of fish in the upper Mississippi River. U.S. Fish and Wildlife Resource Publication. June 1985, LaCrosse, WI. 20 p.

Lowe-McConnell, R. H. 1964. The fishes of the Rupununi savanna district of British Guiana, South America. Part 1. Ecological groupings of fish species and effects of the seasonal cycle on the fish. J. Linn. Soc. Zool. 45(304): 1–103.

1975. Fish communities in tropical freshwaters. Their distribution, ecology, and evolution. Longman, London. 337 p.

Lundberg, J. G., W. M. Lewis, Jr., J. F. Saunders III, and F. Mago-Leccia. 1987. A major food web component in the Orinoco River Channel: evidence from planktivorous fishes. Science 237: 81–83.

Magalhães, C., and I. Walker. 1989. Larval development and ecological distribution of Central Amazon palaemonid shrimps. Crustaceana. (In press)

Margalef, R. 1968. Perspectives in ecological theory. The Univ. of Chicago Press, Chicago, IL. 111 p.

Martins, O. 1982. Geochemistry of the Niger River. Mitt. Geol. Paläont. Inst. Univ. Hamburge SCOPE/UNEP Sonderbd. 52: 357–364.

Marvin, D. E., and A. G. Heath. 1968. Cardiac and respiratory response to gradual hypoxia in three ecologically distinct species of freshwater fish. Comp. Biochem. Physiol. 27: 349–355.

McKnight, J. S., D. D. Hook, O. G. Langdon, and R. L.

Johnson. 1981. Flood tolerance and related characteristics of trees of the bottomland forest of the Southern United States. p. 29–69. *In* J. R. Clark and J. Benforado [ed.] Wetlands of bottomland hardwood forests. — Developments in agricultural and managed forest ecology 11, Elsevier Scientific Publishing Company, Amsterdam, Oxford, New York, NY.

Melack, J. M., and T. R. Fisher. 1983. Diel oxygen variations and their ecological implications in Amazon floodplain lakes. Arch. Hydrobiol. 98: 422–442.

Mills, H. B., W. C. Starrett, and F. C. Bellrose. 1966. Man's effect on the fish and wildlife of the Illinois River. Ill. Nat. Hist. Surv. Biol. Notes 57: 1–24.

Minshall, G. W., K. W. Cummins, R. C. Petersen, C. E. Cushing, D. A. Bruns, J. R. Sedell, and R. L. Vannote. 1985. Developments in stream ecosystem theory. Can. J. Fish. Aquat. Sci. 42: 1045–1055.

Minshall, G. W., R. C. Petersen, K. W. Cummins, T. L. Bott, J. R. Sedell, C. E. Cushing, and R. L. Vannote. 1983. Interbiome comparison of stream ecosystem dynamics. Ecol. Monogr. 53: 1–25.

Morris, L. A., R. N. Langmeier, T. R. Russell, and A. Witt, Jr. 1968. Effects of main stem impoundments and channelization upon the limnology of the Missouri River, Nebraska. Trans. Am. Fish. Soc. 97: 380–388.

Nilsen, H. C., and R. W. Larimore. 1973. Establishment of invertebrate communities on log substrates in the Kaskaskia River, Illinois. Ecology 54: 366–374.

Nord, A. E., and J. C. Schmulbach. 1973. A comparison of the macroinvertebrate aufwuchs in the unstabilized and stabilized Missouri River. Proc. S. D. Acad. Sci. 52: 127–139.

Odum, E. P. 1959. Fundamentals of ecology. W. B. Saunders Co., London. 574 p.

1981. Foreward. *In* J. R. Clark and J. Benforado [ed.] Wetlands of bottomland hardwood forests. — Development in agricultural and managed forest ecology 11, Elsevier Scientific Publishing Company, Amsterdam, Oxford, New York, NY.

Odum, E. P., and A. A. de la Cruz. 1967. Particulate organic detritus in a Georgia salt marsh-estuarine system, p. 383–388. *In* G. H. Lauff [ed.] Estuaries. Publ. 83 of the American Association for the Advancement of Science, Washington D.C.

Paarmann, W., U. Irmler, and J. Adis. 1982. *Pentacomia egregia* Chaud. (Carabidae, Cicindelidae), an univoltine species in the Amazonian inundation forest. Coleopterists Bull. 36: 183–188.

Petrere, M., Jr. 1978. Pesca e esforço da pesca no Estado do Amazonas. II Locais, aparelhos de captura e estatísticas de desembarque. Acta Amazonica 8: 1–54.

1982. Ecology of the fisheries in the River Amazon and its tributaries in the Amazonas State (Brazil). Ph.D. thesis, Univ. of East Anglia, UK. 96 p.

1983. Relationships among catches, fishing effort and river morphology for eight rivers in Amazonas State (Brazil), during 1976–1978. Amazoniana 8: 281–296.

Pflieger, W. L., and T. B. Grace. 1987. Changes in the fish fauna of the Lower Missouri River, 1940–1983, p. 166–177. *In* W. J. Mathews and D. C. Heins [ed.] Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman, OK.

Pianka, E. R. 1970. On *r*- and *K*-selection. Am. Nat. 104: 592–597.

Pieczyńska, E. 1972. Production and decomposition in the eulittoral zone of lakes, p. 271–285. *In* Z. Kajak and A. Hillbricht-Ilkowska [ed.] Proceedings of the IBP-UNESCO Symposium on Productivity Problems of Freshwaters. Kazimierz Dolny, Poland.

Quirós, R., and C. Baigún. 1985. Fish abundance related to organic matter in the Plata River Basin, South America. Trans. Am. Fish. Soc. 114: 377–387.

Remsen, J. V., Jr., and T. A. Parker. 1983. Contribution of river-created habitats to bird species richness in Amazonia. Biotropica 15: 223–231.

Ribeiro, M. C. L. B. 1983. As migrações dos jaraquis (Pisces, Prochilodontidae) no Rio Negro, Amazonas, Brasil. M.S. thesis, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil. 192 p.

Richardson, R. E. 1921. The small bottom and shore fauna of the middle and lower Illinois River and its connecting lakes, Chillicothe to Grafton; its valuation; its sources of food supply; and its relation to the fishery. Ill. Nat. Hist. Surv. Bull. 13: 363–522.

Richey, J. E., J. T. Brock, R. J. Naiman, R. C. Wissmar, and R. F. Stallard. 1980. Organic carbon: oxidation and transport in the Amazon River. Science 207: 1348–1351.

Richey, J. E., E. Salati, and U. Santos. 1985. Biochemistry of the Amazon River: an update. Mitt. Geol. Paläont. Inst. Univ. Hamburg SCOPE/UNEP Sonderbd. 58: 245–257.

Risotto, S. P., and R. E. Turner. 1985. Annual fluctuation in abundance of the commercial fisheries of the Mississippi River and tributaries. N. Am. J. Fish Manage. 5: 557–574.

Roy, D. 1989. Physical and biological factors controlling the distribution and abundance of fish in Hudson/James Bay rivers, p. 159–171. In D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Ruttner, F. 1952. Fundamentals of limnology. Univ. Toronto Press, Toronto, Ont. 242 p.

Salo, J., R. Kalliola, I. Häkkinen, Y. Mäkinen, P. Niemelä, M. Puhakka, and P. D. Coley. 1986. River dynamics and the diversity of Amazon lowland forest. Nature 322: 254–258.

Sandusky, M. J., R. E. Sparks, and A. A. Paparo. 1979. Investigations of declines in fingernail clam (*Musculium transversum*) populations in the Illinois River and Pool 19 of the Mississippi River. Bulletin of the American Malacological Union 1979: 11–15.

Santos, G. M. 1981. Estudos de alimentaçâo e hábitos alimentares de *Schizodon fasciatus* Agassiz, 1829, *Rhytiodus microlepis* Kner, 1859 e *Rhytiodus argenteofuscus* Kner, 1859, do lago Janauacá -AM. (Osteichthyes, Characoidei, Anostomidae). Acta Amazonica 11: 267–283.

Schmidt, G. W. 1973a. Primary production of phytoplankton in the three types of Amazonian waters. II. The limnology of a tropical flood-plain lake in Central Amazônia, Lago do Castanho. Amazonas, Brazil. Amazoniana 4: 139–203.

1973b. Primary production of phytoplankton in the three types of Amazonian waters. III. Primary productivity of phytoplankton in a tropical flood-plain lake of Central Amazonia, Lago do Castanho. Amazonas, Brazil. Amazoniana 4: 379–404.

Schumm, S. A. 1977. The fluvial system. John Wiley and Sons, New York, NY. 338 p.

Sedell, J. R., J. E. Richey, and F. J. Swanson. 1989. The river continuum concept: a basis for the expected ecosystem behavior of very large rivers? p. 49–55. *In* D. P. Dodge [ed.] Proceedings of the International Large River Sysmposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Seger, D. R., and C. F. Bryan. 1981. Temporal and spatial distribution of phytoplankton in the Lower Atchafalaya River Basin, Louisiana, p. 91–101. *In* L. A. Krumholz [ed.] Proceedings of Warmwater Streams Symposium. Allen Press, Lawrence, KS.

Seidenschwarz, F. 1986. Pionervegetation im Amazonasgebeit Perus. Ein pflanzensoziologischer Vergleich von vorandinem Flussufer und Kulturland. Monographs on Agriculture and Ecology of Warmer Climates, Vol. 3, Margraf, Tropical Scientific Books, Gaimerscheim, West Germany. 226 p.

Shelford, V. E. 1954. Some lower Mississippi Valley floodplain biotic communities: their age and elevation. Ecology 15: 126–142.

Sheppe, W., and T. Osborne. 1971. Patterns of use of a floodplain by Zambian mammals. Ecol. Monogr. 41: 179–205.

Sigafoos, R. S. 1964. Botanical evidence of floods and floodplain deposition. U.S. Geological Survey Profesionnal Paper 485-A: 1–35.

Sioli, H. 1984. The Amazon and its main affluents: hydrography, morphology of the river courses, and river types, p. 127–166. *In* H. Sioli [ed.] The Amazon (Monographiae biologicae, Vol 56). Dr. W. Junk, The Hague, Netherlands.

Statzner, B. 1987. Characteristics of lotic ecosystems and consequences for future research directions, p. 365–390. *In* E. D. Schulze and H. Zwolfer [ed.] Potentials and limitations of ecosystem analysis. Ecological Studies 61. Springer-Verlag, Berlin.

Statzner, B., and B. Higler. 1985. Questions and comments on the River Continuum Concept. Can. J. Fish. Aquat. Sci. 42: 1038–1044.

1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwater Biol. 16: 127–139.

Talling, J. F., and J. Rzóska. 1967. The development of plankton in relation to hydrological regime in the Blue Nile. J. Ecol. 55: 637–662.

Teal, J. M. 1962. Energy flow in the salt marsh system of Georgia. Ecology 43: 614–624.

Thompson, J. D. 1973. Feeding ecology of diving ducks on Keokuk Pool, Mississippi River. J. Wildl. Manage. 37: 367–381.

Uetz, G. W., K. L. Van der Laan, G. F. Summers, P. A. Gibson, and L. L. Getz. 1979. The effects of flooding on floodplains in arthropod distribution, abundance, and community structure. Am. Midl. Nat. 101: 286–299.

Vannote, R. L., G. M. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

Welcomme, R. L. 1979. Fisheries ecology of floodplain rivers. Longman, London. 317 p.

1985. River fisheries. FAO Fish. Tech. Pap. 262: 330.

1989. Review of the present state of knowledge of fish stocks and fisheries of African rivers, p. 515–532. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Wharton, C. H., V. W. Lambou, J. Newsom, P. V. Winger, L. L. Gaddy, and R. Mancke. 1981. The fauna of bottomland hardwoods in Southeastern United States. p. 87–160. *In* J. R. Clark and J. Benforado [ed.] Wetlands of bottomland hardwood forests. — Developments in agricultural and managed forest ecology 11, Elsevier Scientific Publishing Company, Amsterdam, Oxford, New York, NY.

Winterbourn, M. J., J. S. Rounick, and B. Cowie. 1981. Are New Zealand stream ecosystems really different?. N. Z. J. Mar. Freshwater Res. 15: 321–328.

Wissmar, R. C., J. E. Richey, R. F. Stallard, and J. M. Edmond. 1981. Plankton metabolism and carbon processes in the Amazon river, its tributaries, and floodplain waters, Peru–Brazil, May–June 1977. Ecology 62: 1622–1633.

Wood, R. 1951. The significance of managed water levels in developing the fisheries of large impoundments. J. Tenn. Acad. Sci. 26: 214–235.

Worbes, M. 1983. Vegetationskundkiche Untersuchungen zweier überschwemmungswälder in Zentralamazonien. Amazoniana 8: 47–65.

1985. Structural and other adaptations to longterm flooding by trees in central Amazonia. Amazoniana 9: 459–484.

1986. Lebensbedingungen und Holzwachstum in zentralamazonischen überschwemmungswäldern. Scripta Geobotanica 17: 112.

Yarbro, L. A. 1983. The influence of hydrological variations on phosphorus cycling and retention in a swamp stream ecosystem, p. 199–221. *In* T. D. Fontaine and S. M. Bartell [ed.] Dynamics of ecosystems. Ann Arbor Science, Ann Arbor, MI.

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Fish and Fisheries of the Mackenzie and Churchill River Basins, Northern Canada

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Abstract

BODALY, R. A., J. D. REIST, D. M. ROSENBERG, P. J. MCCART, AND R. E. HECKY. 1989. Fish and fisheries of the Mackenzie and Churchill river basins, northern Canada, p. 128–144. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The Mackenzie and Churchill rivers drain 1.8×10^6 km² and 3.0×10^5 km², respectively, of subarctic and arctic Canada. Mean annual precipitation in the basins is low, usually <500 mm. The ice-free season lasts for $\simeq$4–8 months. Low rates of phytoplankton primary production ($<$4–80 g $C \cdot m^{-2} \cdot yr^{-1}$) are due to light limitation caused by high suspended sediment loads, by the long period of ice and snow cover, and by low nutrient levels (e.g. total dissolved P 0.2–2.3 $\mu m \cdot L^{-1}$). Knowledge of secondary productivity is limited mainly to commercial fish yields.

The fish faunas of the Mackenzie and Churchill basins are relatively simple: 53 species are native to the Mackenzie and 39 to the Churchill. The faunas are dominated by salmonids and cyprinids. Migratory behavior is characteristic of many of the fish species of importance to fisheries, especially in the Mackenzie basin, where it is often associated with one of the three major delta areas in the basin. Commercial and subsistence fisheries coexist throughout much of both river basins, but most commercial fishing takes place in the Churchill basin and the southern portions of the Mackenzie basin, near to southern Canadian and export markets.

Fisheries management activities in the basins are often hampered by a number of factors. The magnitude of the catch for many commercial and most domestic fisheries is unknown and knowledge of the genetic population structure of species under exploitation is inadequate. Although high standing stocks of large fish are often present, they usually have relatively low rates of biological production. Migratory behavior tends to concentrate fish temporally and spatially, making such populations vulnerable to multiple stresses, including fisheries, during their life cycles.

Although only a moderate amount of industrial activity has taken place in the Mackenzie and Churchill basins, there has been extensive disruption of aquatic systems in the Churchill basin by hydroelectric development. Hydroelectric development will be increasingly important in the future in the Mackenzie basin.

Résumé

BODALY, R. A., J. D. REIST, D. M. ROSENBERG, P. J. MCCART, AND R. E. HECKY. 1989. Fish and fisheries of the Mackenzie and Churchill river basins, northern Canada, p. 128–144. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Les fleuves Mackenzie et Churchill drainent respectivement $1{,}8 \times 10^6$ et $3{,}0 \times 10^5$ km² de terres canadiennes subarctiques et arctiques. Les précipitations annuelles moyennes sont généralement faibles dans ces bassins et se situent normalement en deçà de 500 mm. La saison sans glaces dure de 4 à 8 mois environ. Les faibles taux de la production primaire du phytoplancton ($<$4–80 g $C \cdot m^{-2} \cdot a^{-1}$) s'expliquent par une limitation de l'éclairement due à une charge élevée de matières en suspension, à la longue période où les eaux sont couvertes de glace et de neige et par les faibles teneurs en matières nutritives (P total dissous de 0,2–2,3 $\mu m \cdot L^{-1}$). Nos connaissances de la productivité secondaire se limitent surtout aux rendements en poisson de la pêche commerciale.

La faune ichtyologique des bassins du Mackenzie et du Churchill est relativement simple: il y a 53 espèces indigènes au Mackenzie et 39 espèces indigènes au Churchill. La faune est dominée par des salmonidés et des cyprinidés. Le comportement migratoire caractérise bon nombre d'espèces de poisson importantes pour la pêche, surtout dans le bassin du Mackenzie où il est souvent associé à l'une des trois principales zones à deltas. Des pêches commerciales et de subsistance sont pratiquées concurremment dans la plus grande partie des deux bassins, mais la majorité des pêches commerciales sont réalisées dans le bassin du Churchill et la partie sud du bassin du Mackenzie, à proximité des marchés du sud du Canada et de l'exportation.

Plusieurs facteurs nuisent au bon déroulement des activités de gestion des pêches dans ces bassins. L'importance des prises de bon nombre de pêches commerciales et de la majorité des pêches de subsistance est inconnue et nos connaissances de la structure génétique de la population des espèces exploitées sont insuffisantes. La biomasse des stocks de gros poissons est souvent importante, mais leur taux de production biologique est généralement relativement faible. Le comportement migratoire des poissons a pour effet de favoriser leur concentration temporelle et spatiale, ce qui rend les populations vulnérables à de multiples stress, notamment la pêche, au cours de leur cycle vital.

L'activité industrielle a été relativement peu importante dans les bassins du Mackenzie et du Churchill, mais la mise en valeur hydroélectrique du bassin du Churchill y a fortement perturbé les systèmes aquatiques. Ce type d'aménagement deviendra de plus en plus important dans le bassin du Mackenzie.

Introduction

This paper is a review of information concerning the fish populations, fisheries management, and anthropogenic influences in the Mackenzie and Churchill river basins in northern Canada. The physical and chemical environments in the basins are described as well as energy flow leading to fish production.

The arctic and subarctic river basins discussed in this paper provide some interesting comparisons to temperate and tropical river basins, in addition to the obvious differences in climate. For example, in contrast to temperate and especially tropical systems, aquatic primary and secondary productivity and fish species diversity in the Mackenzie and Churchill basins are very low. However, annual rates of transport of suspended and dissolved materials are remarkably similar between the Mackenzie and more southern rivers (Brunskill 1986). Fishing activities in the Churchill and Mackenzie basins resemble those in tropical basins because both often supply only local needs and both have high proportions of part-time and subsistence fishermen. Finally, industrial development, especially hydroelectric projects, threaten river systems in northern Canada and in tropical areas.

Despite a sparse population base, northern areas of Canada have become the focus for increasing resource-based industrial activities which often conflict directly with resource harvesting such as fishing and hunting. Local residents, especially native people, are highly dependent on such natural resources, both economically and culturally.

Physical Characteristics of the Churchill and Mackenzie Basins

General Description

The Mackenzie River, which flows north into the Arctic Ocean, is the longest in Canada and its basin contains several of Canada's largest lakes (Fig. 1, 2, 3). The Mackenzie basin extends over 15° of latitude (54–69°N) and 37° of longitude (103–140°W) (Fig. 1). The Churchill River, flowing eastward into Hudson Bay, is also an arctic drainage. The Churchill basin is $\simeq 1/6$ the area of the Mackenzie basin and it extends over 6° of latitude (53–59°N) and 19° of longitude (94–113°W).

The Mackenzie River has a mean annual flow of 9 500–11 000 $\mathrm{m^3{\bullet}s^{-1}}$ at the Mackenzie Delta and flows can reach 22 000 $\mathrm{m^3{\bullet}s^{-1}}$ there. The average discharge of the Churchill River is 637 $\mathrm{m^3{\bullet}s^{-1}}$ at the Saskatchewan–Manitoba border, 1 011 $\mathrm{m^3{\bullet}s^{-1}}$ at Missi Falls, and 1 120 $\mathrm{m^3{\bullet}s^{-1}}$ at Red Head Rapids, 70 km upstream of its outlet into Hudson Bay (Churchill River Study (CRS) 1976; G. K. McCullough, Freshwater Institute (FWI), personal communication). Natural high-water levels occur in spring on the Mackenzie as a result of rapid runoff from the mountains, but high water is delayed until July and August in the Churchill because of the relatively large amount of storage in lakes (CRS 1976).

The Mackenzie system includes seven major rivers (Peace, Athabasca, Slave, Liard, Great Bear, Peel, and Mackenzie proper). The three largest lakes in the Mackenzie basin are Great Bear (surface area 3.1×10^4 km^2), Great Slave (2.7×10^4 km^2), and Athabasca (7.9×10^3 km^2) (Mackenzie River Basin Committee (MRBC) 1981; Brunskill 1986). The Churchill system includes two major rivers (Reindeer and Churchill proper). The three largest lakes in the Churchill basin are Reindeer (surface area 5.6×10^3 km^2), Southern Indian (2.4×10^3 km^2), and Wollaston (2.1×10^3 km^2). Southern Indian and Reindeer lakes have been impounded for hydroelectric purposes (CRS 1976; Newbury et al. 1984).

The Mackenzie River drains parts of four physiographic regions: the Western Cordillera, the Interior Plain, the Precambrian Shield, and the Arctic Coastal Plain (the Mackenzie Delta) (Fig. 1). The Churchill River drains parts of the Interior Plain, the Precambrian Shield, and the Hudson Region (Arctic Plain) (Fig. 1).

Glacial History

Almost all of the Churchill and Mackenzie basins were covered by ice during Wisconsin glaciation (Fig. 1). Aquatic biota survived glaciation south of the ice sheet in the continental USA, in unglaciated portions of the central Yukon and Alaska, and also in the ice-free corridor from the South Nahanni River to the western slopes of the Richardson Mountains (Prest 1970). Deglaciation began 14 000–12 000 BP and was complete by 8000 BP. Numerous large proglacial lakes bordered the ice margins at various times and along with overflow of drainage divides, flow reversals, and stream headwater capture, allowed for reinvasion of newly deglaciated areas by aquatic biota (Lindsey and McPhail 1986).

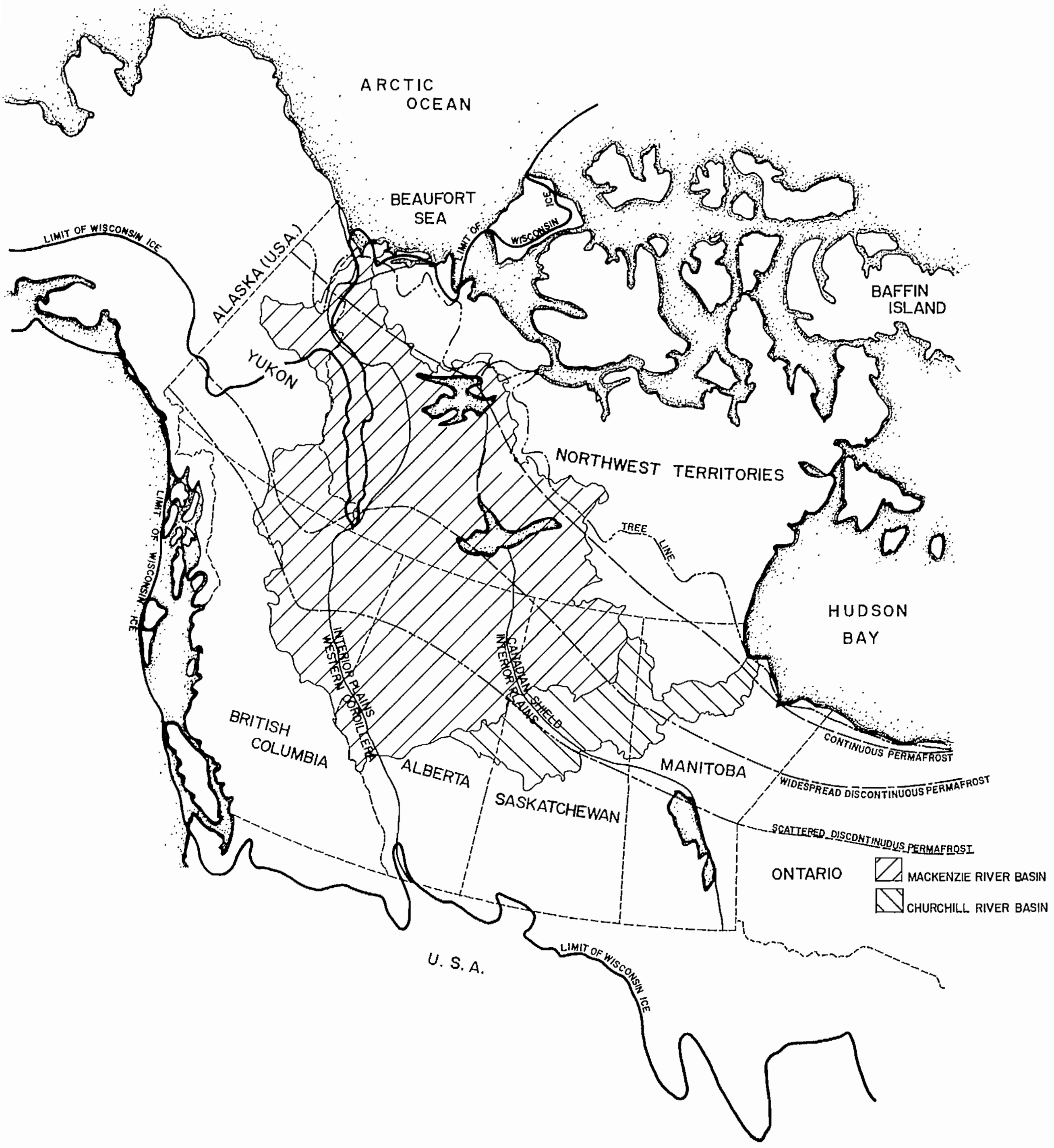

FIG. 1. Northwestern North America showing limits of Mackenzie basin, Churchill basin, physiographic zones, political boundaries and climatological features.

Climate and Runoff

The climate of the Mackenzie basin is either tundra (northeastern region and the high Western Cordillera) or subarctic (remainder of basin) (Rosenberg and Barton 1986). The entire Churchill basin has a subarctic climate (CRS 1976). Both basins are characterized by large differences between winter and summer temperatures. In the upper Mackenzie basin, mean daily temperatures vary from 16 to 21°C in July to -20 to -25°C in January. In the lower Mackenzie basin, mean daily temperatures vary from 10 to 16°C in July to -23 to -29°C in January. In the Churchill basin, the July mean daily temperature of 17°C is fairly uniform across the basin, whereas January mean daily temperatures vary from -18°C (Lac la Biche, AB) to -29°C (Brochet and Churchill, MB). River channels and lakes in the Churchill basin are ice covered for about 5 to 8 months of the year. In the Mackenzie basin, the period of ice cover ranges

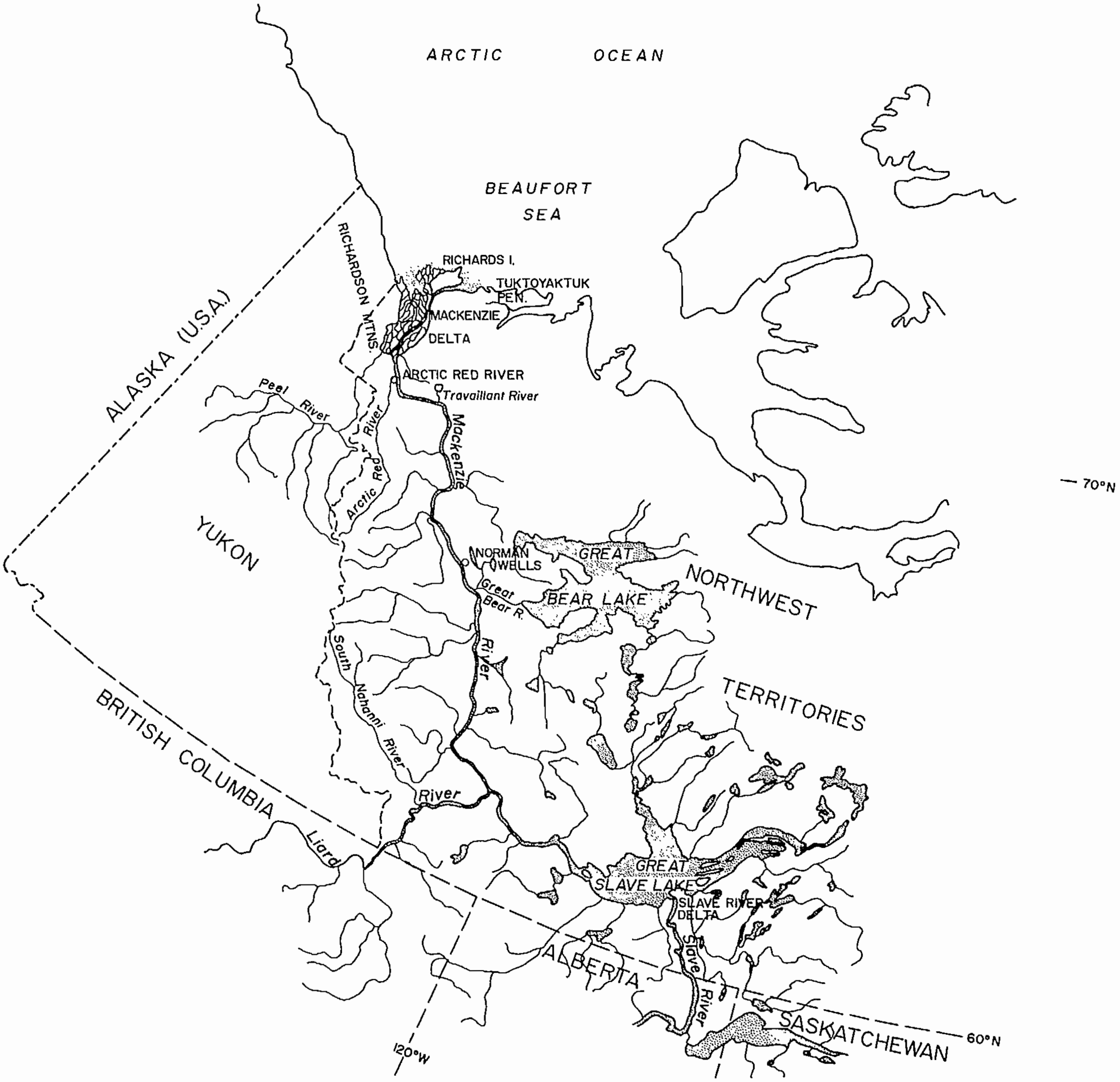

FIG. 2. Lower Mackenzie basin.

from about 4 months in the southern parts of the basin to over 8 months in the northern parts. Both river basins are located largely within the zones of discontinuous or widespread permafrost (Fig. 1).

The Mackenzie basin receives significantly more precipitation than the Churchill basin. East of the Mackenzie River, annual precipitation is 250–400 mm and maximum snow coverage equals 500–760 mm (Brunskill 1986). In the mountainous western part of the basin, mean annual precipitation is 500–1600 mm and snow cover equals 1020–1520 mm. Precipitation is fairly uniform throughout the Churchill basin, ranging from 410–460 mm$\cdot$yr^{-1} of which >250 mm falls as rain (CRS 1976). Runoff in the Mackenzie basin is 25–50 % of annual precipitation in the Interior Plain, approximately 30 % in the Precambrian Shield, and 40–70 % in the Western Cordillera (Brunskill 1986).

Suspended Sediments and Dissolved Nutrients

The proportion of the Churchill and Mackenzie rivers draining the various physiographic regions is quite different. The Churchill basin is predominantly Canadian Shield whereas the Mackenzie basin is predominantly Interior Plain (Fig. 1). Runoff from the Precambrian Shield in both basins is quite dilute whereas runoff from the Interior Plain has moderate to high concentrations of dissolved salts because of more soluble surface and subsurface bedrock (Table 1). Rivers of the Western Cordillera in the Mackenzie basin transport large quantities of suspended sediment primarily reflecting high erosion rates in the area. Most N and P is in particulate form in Western Cordilleran rivers having significant runoff. Lakes throughout the upper part of the Churchill basin act as sediment traps for suspended sediment, so sediment contributed by the Churchill

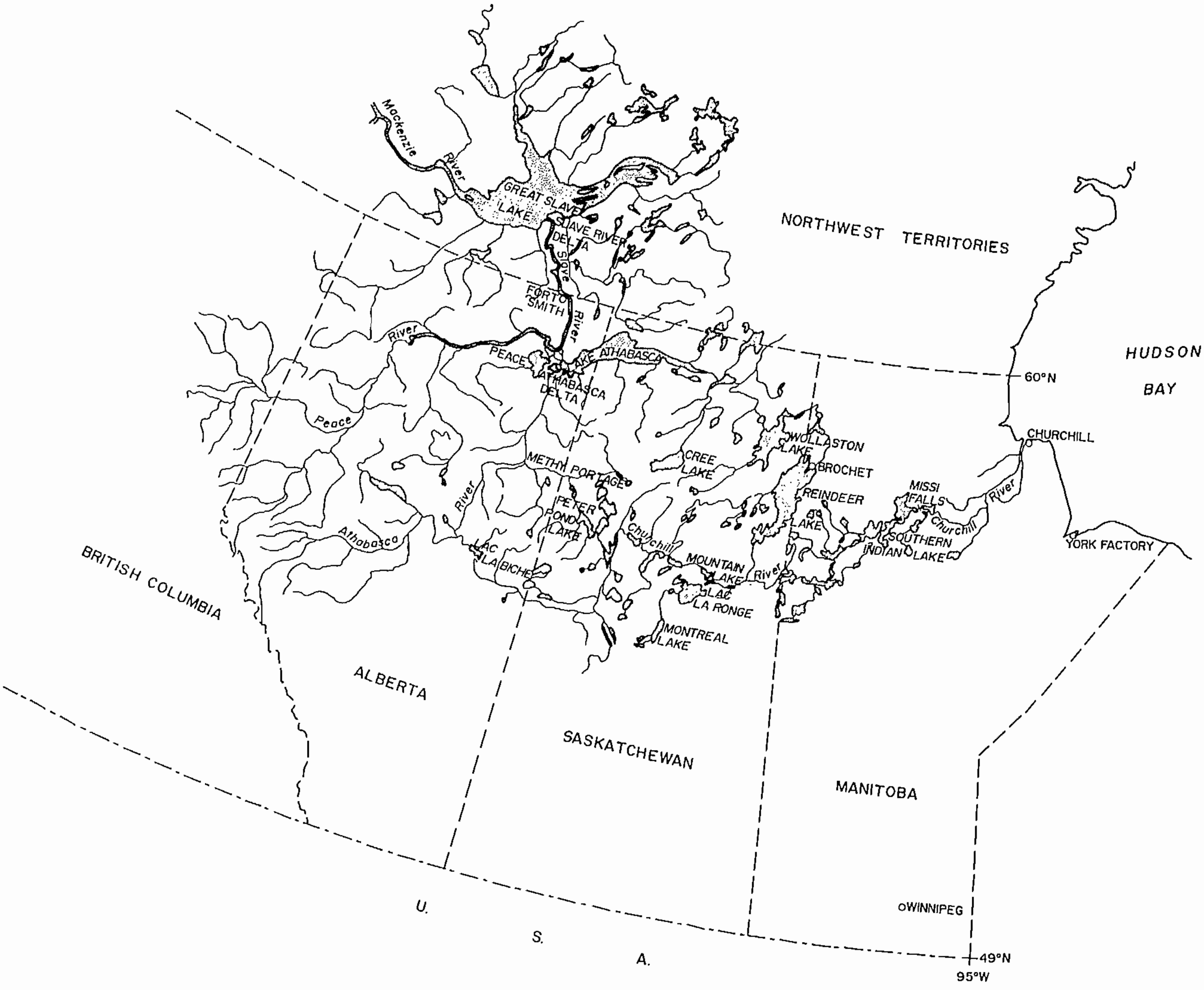

FIG. 3. Upper Mackenzie and Churchill basins.

River to Hudson Bay is minimal and largely reflects what has been picked up along the lower Churchill (Table 1). In the Mackenzie basin, most of the sediment transported by the Peace and Athabasca rivers from the Western Cordillera is trapped in the Peace-Athabasca Delta and other intervening deltas and lakes, so that the sediment load delivered to the Mackenzie Delta originates mainly in the rivers of the northern portion of the Western Cordillera region (Table 1; Brunskill 1986).

Energy Flow

The amount of information on primary and secondary production in the lakes and channels of the Mackenzie and Churchill rivers is extremely limited. Information tends to decrease with increasing trophic level.

Primary production in the Mackenzie and Churchill rivers is generally light-limited during the open-water season as a result of relatively high suspended sediment concentrations. Even the Churchill River, which is relatively transparent to light because of its lower sediment load, is light-limited as it enters Southern Indian Lake (Healey and Hendzel 1980). Light penetration increases in lakes as suspended load settles. Then, primary production can become nutrient-limited. In Southern Indian Lake, prior to impoundment and Churchill River diversion (Newbury et al. 1984), nutrient deficiency increased between inflow and outflow and in isolated bays (Healey and Hendzel 1980; Hecky and Guildford 1984). The western basin of Great Slave Lake is much more turbid and much less nutrient deficient than the eastern basins because of nutrient and sediment loading by the Slave River (Fee et al. 1985). A similar relationship is evident for lakes in the Mackenzie Delta having different degrees of connection to the river channel (Fig. 4). As water clarity improves with decreasing connectedness with the river channel, phytoplankton primary productivity increases by nearly a factor of three until the lakes become severely phosphorus deficient (Fig. 4). The long season of ice and snow cover severely limits light penetration and aquatic primary production for much of the year.

Phytoplankton primary production stongly influences the fisheries yields of many lakes (Fig. 5; Oglesby 1977). Low values of primary productivity are typical for waters of the Mackenzie and Churchill basins. Primary production ranges from <4 g $C \cdot m^{-2} \cdot yr^{-1}$ in the eastern arm of Great Bear Lake (Schindler 1972) and <10 $g \cdot m^{-2} \cdot yr^{-1}$ in the east-

TABLE 1. Average concentrations of chemical variables for rivers and lakes in different physiographic regions of the Mackenzie and Churchill basins (data from Koshinsky 1965, 1968; Cleugh 1974; Davis 1976; Dean 1980; Brunskill 1986). TDS = total dissolved solids; TDN = total dissolved nitrogen; TDP = total dissolved phosphorus; N/A = not available.

Rivers	Suspended sediment load (10^3 kg•km^{-2}•yr^{-1})	TDS (mg•L^{-1})	Conductivity (μmhos•cm^{-1})	pH	TDN (μmoles•L^{-1})	TDP (μmoles•L^{-1})
Mackenzie Basin						
Precambrian Shield	<3[e]	22	45	6.8–7.6	22	0.25
Interior Plain	56	449	578	7.0–8.1	53	2.30
Western Cordillera	101	198	347	7.5–8.2	45	1.50
Lower Mackenzie River[a]	68	153	269	8.0	43	0.50
Churchill Basin						
Precambrian Shield[b]	<3	17	28	7.4–7.6	32	0.16
Interior Plain[c]	N/A	80	138	7.0–8.0	55	0.55
Lower Churchill River[d]	0.4	79	81	7.2–8.0	23	0.64

Lakes	No. of lakes	TDS (mg•L^{-1})	Conductivity (μmhos•cm^{-1})	pH	TDN (μmoles•L^{-1})	TDP (μmoles•L^{-1})
Mackenzie Basin						
Precambrian Shield	17	44	86	5.9–8.3	33	0.37
Interior Plain	10	130	206	6.3–8.5	32	0.40
Western Cordillera	11	135	182	7.1–8.5	10	N/A
Churchill Basin						
Precambrian Shield	12	52	58	6.7–7.5	31	0.25
Interior Plain	7	168	275	7.2–8.4	N/A	N/A

[a] Mackenzie and Peel River inputs to Beaufort Sea as measured near mouth of the Mackenzie Delta.

[b] Reindeer River at Atik Falls.

[c] Churchill River at Otter Falls.

[d] Churchill River at Missi Falls.

[e] Based on Precambrian Shield in the temperate zone.

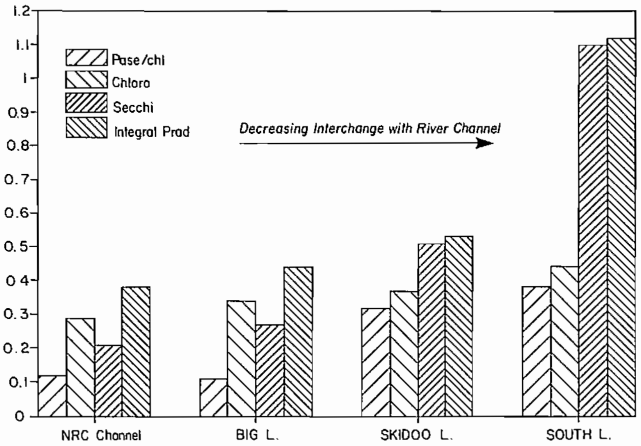

FIG. 4. Relationship among water clarity, primary production, algal biomass and nutrient demand in a series of lakes with decreasing interchange with a network channel (the NRC channel) in the Mackenzie Delta. Data are from E. J. Fee and S. J. Guildford, FWI, personal communication. Pase/chl = alkaline phosphatase activity (μM P•h^{-1}•(μg chl a)$^{-1}$; values >0.005 indicate severe P deficiency; Healey and Hendzel 1980). Chloro = chlorophyll (μg•L^{-1}), Secchi = Secchi disk transparency (m). Integral Prod = Integral phytoplankton productivity (mg C•m^{-2}•d^{-1}). Actual values of Pase/chl have been multiplied by 10 while Integral Prod and chl have been divided by 10 so that all values fit on the same scale.

ern basin of Great Slave Lake (Schindler 1972), to about 30 g•m^{-2}•yr^{-1} in the western basin of Great Slave (Fee et al. 1985) and about 80 g•m^{-2}•yr^{-1} in Southern Indian Lake (Hecky and Guildford 1984) (Fig. 5). The historical yields from Great Slave and Southern Indian lakes fall somewhat above that expected for large lakes, given their phytoplankton production (Fig. 5). The riverine influence on these lakes may contribute to their higher than expected yield because the rivers supply organic carbon from terrestrial sources which may be important in lacustrine food chains.

The role of primary productivity from non-phytoplankton sources may be especially evident in the lakes of the Mackenzie Delta. These lakes have very low annual phytoplankton productivities (4–10 g C•m^{-2}•yr^{-1}). However, they are shallow and many have productive aquatic macrophyte communities. For example, South Lake, in the Mackenzie Delta, has approximately 30 g C•m^{-2}•yr^{-1} of macrophyte production (D. Mathew and R. E. Hecky, FWI, unpublished data) which is >3× the phytoplankton productivity of the lake (Fig. 4). The production of epipelon (algae living on the sediment) and periphyton (algae attached to hard substrata)combined is approximately equal to the phytoplankton productivity (S. J. Guildford and D. Mathew, FWI, unpublished data). These shallow delta lakes, and those on the Tuktoyaktuk Peninsula, the abandoned Pleistocene delta of the Mackenzie, support the feeding of large populations of anadromous coregonids (Bond and Erickson 1985, and see below). Given the low phytoplankton productivities of these lakes, the macrophyte communities must be important in supporting fish populations.

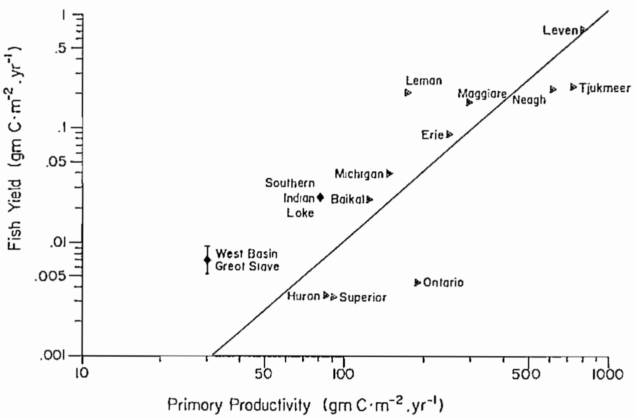

FIG. 5. Fish yield as a function of primary productivity. The solid line is from Oglesby (1977). Large, north temperate lakes from Oglesby's data set and Great Slave and Southern Indian lakes are indicated individually (after Fee et al. 1985).

TABLE 2. Summary, by family, of numbers of fish species native to the Mackenzie and Churchill basins. Lower Mackenzie includes mainstem and tributaries of Mackenzie River from the Mackenzie Delta upstream to include Great Slave Lake and its local tributaries. Upper Mackenzie includes Slave, Peace and Athabasca Rivers and their tributaries. Data for Mackenzie from Lindsey and McPhail (1986); for Churchill from Atton and Merkowsky (1983) and Crossman and McAllister (1986). Introduced species omitted.

	Mackenzie Basin			
Family	Lower	Upper	Total	Churchill Basin
Petromyzontidae	2	1	2	0
Acipenseridae	0	0	0	1
Salmonidae				
Pacific salmon (*Oncorhynchus*)	3	1	3	0
Trout (*Salmo*)	1	1	1	0
Char (*Salvelinus*)	4	3	4	3
Whitefishes (*Coregoninae*)	9	7	10	4
Grayling (*Thymallus*)	1	1	1	1
Total Salmonidae	18	13	19	8
Osmeridae	2	0	2	0
Hiodontidae	1	1	1	1
Esocidae	1	1	1	1
Cyprinidae	7	13	13	11
Catostomidae	2	3	3	3
Gadidae	1	1	1	1
Gasterosteidae	2	2	2	3
Percopsidae	1	1	1	1
Percidae	1	3	3	6
Cottidae	4	4	5	3
Total species	42	43	53	39

Fish Populations

Species Composition and Origin

Fifty-three species of fish are native to the Mackenzie basin (Table 2). The number of species is similar in the lower (42) and upper (43) regions of the basin although the composition differs considerably. The lower Mackenzie contains 18 species of salmonids compared to 13 in the upper Mackenzie; the species absent in the upper part of the basin are those which are sometimes anadromous. Thirteen cyprinid species are present in the upper Mackenzie but only seven have been reported in the lower region.

Thirty-nine species occur in the Churchill basin (Table 2). The distribution of these species varies: 18 occur over the entire basin, 11 occur in the upper reaches only, four are restricted to the lower region, and two are coastal only (Crossman and McAllister 1986). Four others have been found only recently and distributional data are lacking for them.

Much of the difference in the number of species between the Mackenzie and Churchill basins (53 vs 39) is accounted for by the greater representation of salmonids in the Mackenzie (19 vs 8). The Churchill system also lacks two osmerids (coastal species), two cyprinids, and two cottids, but has three more percids and one more each of gasterosteids and acipenserids than the Mackenzie system. Of the 29 species common to the two basins (Table 2), 24 are shared with the lower Mackenzie region and 28 are shared with the upper Mackenzie region. Therefore, species composition in the Churchill and upper Mackenzie region are most similar. Most of the differences in fish species composition of these areas can be explained by post-glacial dispersal patterns (Crossman and McAllister 1986; Lindsey and McPhail 1986).

Present differences in basin size, river discharge and the diversity of habitat types available probably are the major reasons for differences in the number of species in the two basins (Welcomme 1985; Livingstone et al. 1982). The Mackenzie has a complex basin that covers a large latitudinal range, includes six large rivers, one of the largest estuarine deltas in the world, several major freshwater deltas, and three of the world's largest lakes. The Churchill, in contrast, is a less complex basin that crosses a small latitudinal range. Its lower reaches, which run through the Precambrian Shield, appear to offer limited habitat for fishes, especially anadromous salmonids (see below). There are fewer fish species in both the Churchill and Mackenzie basins than predicted for African rivers on the basis of discharge (Livingstone et al. 1982) and many fewer than predicted for tropical and temperate rivers on the basis of watershed area (Welcomme 1985). However, the difference between the two Canadian basins is proportional to differences in their discharges and watershed areas.

Of the total species complement for the two basins (63 species), relatively few are intensively or extensively fished, and most of these are salmonids (Table 3). Other species also may be involved locally, but the 14 listed in Table 3 are the most important.

Fish Migrations

Migration offers adaptive advantages to fish and is relevant to fisheries and their management. Fish are able to maximize their utilisation of habitat by selecting the best spawning, feeding, and overwintering areas within their range even though these may be widely separated. Fish migrations often result in large runs of fish concentrated into small channels, making the fish vulnerable to overfishing. Stocks are often subject to multiple stresses, including har-

TABLE 3. Presence (+) and absence (−) of fish species of commercial, subsistence and/or sport fishery importance native to the Mackenzie and Churchill basins. Delineation for upper and lower Mackenzie basin as for Table 2. Data from Lindsey and McPhail (1986), Atton and Merkowsky (1983) and Crossman and McAllister (1986).

Scientific name	Common name	Mackenzie Basin Lower	Mackenzie Basin Upper	Mackenzie Basin Total	Churchill Basin
Acipenser fulvescens	Lake sturgeon	−	−	−	+
Salmo gairdneri	Rainbow trout	+	+	+	−
Salvelinus alpinus	Arctic char	+	−	+	+
Salvelinus fontinalis	Brook trout	−	−	−	+
Salvelinus namaycush	Lake trout	+	+	+	+
Coregonus clupeaformis	Lake whitefish	+	+	+	+
Coregonus nasus	Broad whitefish	+	−	+	−
Coregonus autumnalis	Arctic cisco	+	−	+	−
Stenodus leucichthys	Inconnu	+	+	+	−
Thymallus arcticus	Arctic grayling	+	+	+	+
Hiodon alosoides	Goldeye	+	+	+	+
Esox lucius	Northern pike	+	+	+	+
Lota lota	Burbot	+	+	+	+
Stizostedion vitreum	Walleye	+	+	+	+

vesting, at different points in their life cycles.

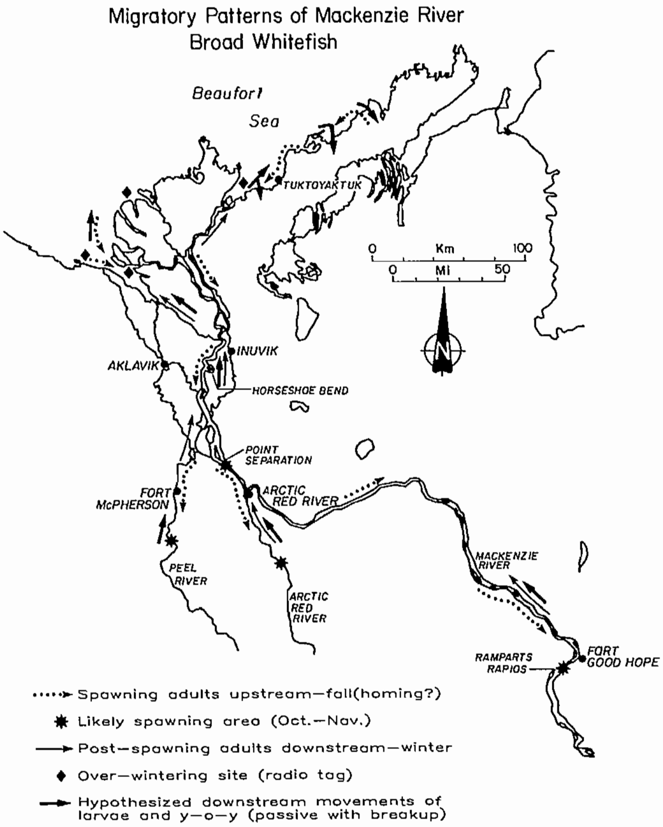

FIG. 6. Generalized migration routes of the broad whitefish (*Coregonus nasus*) in the lower Mackenzie River area.

The Mackenzie Basin — Much of the following is based on McCart's (1986) review of available information on large-scale movements of fish in the Mackenzie River system. Within the system there are long reaches without any major barrier to fish movements and even relatively small species such as Arctic grayling and Arctic cisco travel extensively. In the lower Mackenzie River there are six major anadromous species, all of which are salmonids (Arctic char, Arctic cisco, least cisco (*Coregonus sardinella*), lake whitefish, broad whitefish, and inconnu), which undertake complex migrations. Although migration patterns are highly variable among species, and definitive knowledge is lacking on any one species, the movements of the broad whitefish (Fig. 6), a species favoured by subsistence fishermen, are perhaps the best understood. Sexually mature fish migrate upstream in the early autumn and spawn in the mainstem Mackenzie (at Ramparts Rapids, at Point Separation, and likely also near the town of Arctic Red River) and in major tributaries such as the Peel and Arctic Red rivers (Hatfield et al. 1972; Stein et al. 1973; Chang-Kue and Jessop 1983; J. D. Reist, unpublished data). Spawning occurs at or near freeze-up from late October to November. Spent adults return to channels in the outer Mackenzie Delta to overwinter (K. T. J. Chang-Kue, FWI, personal communication). Larval fish are probably flushed out of the Mackenzie River by the spring freshet, and move northeastward with prevailing currents into the southern Beaufort Sea along the Tuktoyaktuk Peninsula (Bond and Erickson 1985). There are large upstream migrations of young-of-the-year and juveniles into the shallow lake systems of the Tuktoyaktuk Peninsula and Richards Island after ice break-up on creeks and lakes (Bond 1982; Bond and Erickson 1985; Lawrence et al. 1984). These lakes are utilized as summer feeding areas and overwintering habitat until fish reach the age of first maturity. Also, shortly after ice break-up, there are large downstream migrations of juveniles and fish which will spawn the same year (Bond and Erickson 1985). Juveniles moving into and out of these lake systems may migrate regularly into the Mackenzie Delta and back, perhaps on a yearly basis. Movements of large numbers of fish take place along the nearshore environment of the Tuktoyaktuk Peninsula (Bond 1982; Bond and Erickson 1985). However, after first spawning most adults appear to restrict their movements to between the Mackenzie Delta for feeding and overwintering and upstream spawning areas (K. T. J. Chang-Kue, FWI, unpublished data).

Movements of the Arctic cisco are the most extensive of any of the anadromous coregonids. The Arctic cisco has the widest marine distribution of these species (McCart 1986), and is the only one which spawns in large numbers upstream of Ramparts Rapids, in the Great Bear (McCart 1982) and Liard (McLeod and O'Neil 1983) rivers. Gallaway et al. (1983) suggested that Arctic cisco which are found as far west as Point Barrow in Alaska originate in the Mackenzie River. If so, an individual fish returning from the outermost reaches of its coastal distribution to the uppermost part of the known spawning grounds on the Liard River might travel ≃4800 km (2100 km coastal and 2700 km in rivers) return distance. At the other extreme are species such as lake whitefish and inconnu which remain primarily in the Mackenzie Delta (Bond 1982; Bond and Erickson 1982, 1985; Lawrence et al. 1984).

Freshwater species resident in the lower Mackenzie River may also undertake extensive migrations. Best known are Arctic grayling populations which spawn in small tributaries of the Mackenzie River near Normal Wells, but which feed during the summer and overwinter in the Great Bear River and Great Bear Lake (Chang-Kue and Cameron 1980). In this case, spawning and overwintering locations are located as far as 280 km apart.

Examples of large scale, wholly freshwater migrations in the upper Mackenzie River include: (1) fall spawning migrations of cisco (*Coregonus artedii*), lake whitefish, and inconnu from Great Slave Lake, through the Slave River Delta and upstream on the Slave River as far as Fort Smith, a distance of 200 km (Tripp et al. 1981); (2) the complex movements of goldeye in the Peace-Athabasca Delta and adjacent rivers (Donald and Kooyman 1977; Kristensen and Summers 1978; Bond 1980; Kristensen 1980); (3) movements of walleye between the Peace-Athabasca Delta and Lake Athabasca, an annual circuit of as much as 600 km (Dietz 1973; Ott and Sekerak 1976; Summers 1978; Kristensen 1979; Bond 1980); and (4) spawning migrations of lake whitefish (fall) and longnose suckers (*Catostomus catostomus*) (spring) which journey 260 km from Lake Athabasca to spawn in the Slave River at the base of Mountain and Cascade Rapids (Tripp and McCart 1979; Bond 1980; McCart et al. 1982).

The Churchill River Basin — In the Churchill basin, the existence of anadromous or wholly freshwater migrations is poorly documented. However, it appears that migrations are limited both in extent and in the number of fish involved. Small numbers of anadromous lake whitefish, cisco, and brook trout utilize the lower Churchill River (Lower 1915; Walker 1931; Manitoba Department of Natural Resources, unpublished data). The lake whitefish and cisco are presumably utilizing salt-water areas in Hudson Bay for feeding in the spring and summer as they do in the James Bay region (Dymond 1933; Morin et al. 1981). Wholly freshwater migrations of walleye have been documented in Lac la Ronge and Southern Indian Lake (Rawson 1957a; Bodaly 1980). Although both studies showed movements of up to 160 km for individual fish, most tagged walleye were recaptured within about 10 km of their spawning area. Bodaly et al. (1984) speculated that prior to the construction of a dam at the outlet of Southern Indian Lake, lake whitefish may have migrated between the lake and areas downstream on the Churchill River; the number of fish involved in these movements was not known. The lack of noteworthy freshwater migrations in the Churchill River may be due to a general lack of anadromous coregonids (compared to those found in the lower Mackenzie) and a lack of major freshwater delta habitats in the basin. Many of the migrations in the Mackenzie basin are associated with the large Peace–Athabasca, Slave, and Mackenzie deltas. Fish probably migrate away from deltas for spawning to avoid areas of high sedimentation and the lack of deltas in the Churchill basin has meant a lack of selection for such migrations. Also, deltas probably provide productive feeding habitat for the young and juveniles of some species (see above).

Fisheries of the Mackenzie and Churchill Basins

This section will describe the commercial and subsistence (domestic) fisheries of the Northwest Territories (NWT), Alberta, Saskatchewan, and Manitoba portions of the Mackenzie and Churchill river basins. Three types of fisheries will be distinguished: export commercial (those producing fish for sale outside the region), local commercial (those producing fish for local sale), and subsistence (those producing fish for personal use). These three types of fisheries differ markedly with respect to the amount of regulatory attention given them by management agencies.

Both commercial and subsistence fishing in northern Canada are carried out mainly by native peoples, that is, Indians, Inuit, and persons of mixed blood. Fishing is an important cultural tradition and not strictly an economic activity. Although subject to different regulations, commercial and subsistence fishing activities are closely intertwined because they are often conducted by the same people at the same time. Depending on factors such as markets, transportation costs, and species caught, portions of a given catch may either be sold commercially or used domestically. Fishermen often obtain commercial permits although only a small part of the catch is actually sold.

Commercial and subsistence fishing in the Mackenzie and Churchill basins is conducted almost exclusively by gillnetting. There are generally two distinct fishing seasons: (1) a summer season which usually commences after spring-spawning fish have spawned and ends when ice forms on lakes and rivers, and (2) a winter season which commences after winter ice is thick enough for travel. Summer fisheries are conducted mainly from small to medium-sized boats (3–10 m in length), whereas winter fisheries are usually conducted using power snowmobiles.

Commercial Fisheries

Most of the commercial fisheries in both the Churchill and Mackenzie basins are in lakes and riverine lakes rather than in river channels. The total allowable catches of most commercial fisheries are controlled by quota systems. Quotas generally apply to areas rather than to individuals, so that fishing stops for all fishermen when the area quota is reached. The species composition of the catch is not usually controlled. In many of the commercial fisheries whose catches are destined for local sale, especially in the NWT, there is no control over total catches because the only regulatory system is year-end questionnaires. The size of fish caught in commercial fisheries is regulated indirectly by controlling the allowable minimum mesh sizes for gillnets. Also, seasons are usually regulated and the amount (length) of gillnet which can be fished under each commercial fishing licence is limited. Export commercial fisheries are all located in the Churchill basin and the southern part of the Mackenzie basin, near to transportation routes. Great Slave Lake is the approximate northern limit for export fisheries in the Mackenzie basin. The magnitude of these export fisheries is accurately documented.

Although the Mackenzie basin is six times larger than the Churchill basin, the paucity of export fisheries in the central and northern areas of the Mackenzie has resulted in much smaller export fisheries production than in the Churchill. There are 160 export commercial fisheries, defined as fisheries which have a recorded catch for at least one season over the period 1973–81, in the Mackenzie basin and 368 in the Churchill basin (Department of Fisheries and Oceans, Economics and Marketing Directorate, Winnipeg, MB, unpublished data). The total annual catch for export fisheries in the Churchill basin has averaged $\simeq 4.21 \times 10^3$ t over a 9-yr period (1973–74 to 1981–82), whereas that for the Mackenzie basin has averaged only $\simeq 2.82 \times 10^3$ t over the same period. The winter fisheries of the Mackenzie basin are proportionately more important than those in the Churchill basin. They produced 35 % of annual production in the Mackenzie basin as compared to 15 % of annual production in the Churchill basin (Department of Fisheries and Oceans, Economics and Marketing Directorate, Winnipeg, MB, unpublished data).

The species mix is generally similar for the commercial fisheries of the two areas. The fisheries are highly selective and most species are discarded because of low market value. The dominant species is lake whitefish, which comprises 56 and 50 % of the catch by weight in the Mackenzie and Churchill basins, respectively. The walleye is more important in the Churchill basin, where it comprise $\simeq$ 16 % of the annual catch, as compared to only 5 % of the catch in the Mackenzie basin. The other two major export species are pike (21 % of Churchill basin catch; 13 % of Mackenzie basin catch) and lake trout (8 and 12 %, respectively).

Production for most of the export commercial fisheries in both basins is quite sporadic. In the Churchill basin, an average of only 112 of the 368 fisheries, or 30 %, produced a recorded catch in the summer seasons 1973–81 and only 71 of the 368 fisheries, or 19 %, produced a recorded catch in the winter seasons 1973–74 to 1981–82. In the Mackenzie basin, for the same period, an average of only 36 of 160 fisheries, or 22 %, produced a recorded catch in the summer, and only 44 fisheries, or 28 %, produced a recorded catch in the winter.

Fishing for local sale is conducted throughout the two basins and is the only type of commercial fishery in the lower Mackenzie. Although most of these fisheries in the Churchill basin and in the southern part of the Mackenzie basin are conducted in lakes and riverine lakes, those in the lower Mackenzie take place largely in river channels. Catches of fish sold locally are poorly recorded, even though there is a national requirement for the recording of all commercial catches. This requirement is often not enforced in many of the provinces. In NWT, all fishermen who hold commercial licences are required, annually, to respond to a questionnaire and report all catches. However, reporting is not usually complete, reported catches depend on the memory of individual fishermen, and the accuracy of reported catches is rarely investigated.

Subsistence Fishing

Subsistence fishing is also conducted throughout the two basins, particularly in the vicinity of native communities. There are usually no regulations for total catch or season. In the NWT, there is no control of mesh size or length of net used for subsistence fisheries, but these aspects are regulated in Alberta, Saskatchewan and Manitoba. As in the case of fisheries for local sale, most subsistence fishing in the Churchill basin and southern part of the Mackenzie basin is conducted in lakes and riverine lakes whereas fishing in the lower Mackenzie takes place largely in river channels. The magnitude of subsistence catches is even less well-documented than catches for local sale. In the NWT there is no statutory requirement for Inuit, Indians, and persons of mixed blood to have permits to fish domestically. In Alberta, Saskatchewan, and Manitoba, all subsistence fishermen are required by law to have permits. Harvest levels are usually determined only by specific studies at particular communities at particular times. Methods have usually differed from study to study and results are highly variable. In the NWT, total community harvests (commercial plus subsistence) are determined by extrapolating catches reported on questionnaires returned by commercial licence holders. The extrapolated catch becomes the estimated upper limit for the community whereas the actual catch reported by commercial licence holders becomes the estimated lower limit. McCart and Den Beste (1979) and Bodaly (1986) reviewed of the magnitude of subsistence fisheries in northern Canada. Domestic fisheries, like their commercial counterparts, are highly seletive with regard to species retained.

Fisheries Management

The level of involvement of fisheries management agencies in the fisheries of the Mackenzie and Churchill basins depends strongly on the size and importance of the fishery. In general, only the larger export commercial fisheries receive significant attention; subsistence fisheries receive the least attention. The recording of catches has been dealt with in the previous section. This section will discuss stock definition studies, approaches to stock management, examples of two fisheries, and some economic considerations.

Stock Definition

Effective management of fish populations requires that the management units coincide with the smallest units of population structure, or genetic stocks. Few studies have been conducted in the Mackenzie or Churchill basins with the objective of comprehensively determining the stock structure of a particular species, especially utilizing genetic characteristics of spawning aggregations, the least ambiguous approach to the problem. Despite this, considerable evidence indicates genetic structuring of fish populations in lakes, rivers and deltas in the two basins (seven species in 13 locations) (Table 4). In some instances, structuring of populations in close proximity was evident (e.g. lake trout samples from Great Bear Lake taken about 13 km apart; Miller and Kennedy 1948). Also, genetic structuring of populations was evident despite substantial movements and non-spawning intermingling of fish (e.g. walleye in Lac la

Ronge; Rawson 1957a). In general, data on stock structure are available only for the largest and most important fisheries in the Churchill and Mackenzie basins (Table 4). Even so, most data have been gathered incidentally to other studies. There are few studies of the genetic stock structure of river populations.

Two case studies which have utilized genotypic information are especially relevant here. The first concerns the relationship between stock structure of lake whitefish and the impoundment of Southern Indian Lake (SIL) and the diversion of the Churchill River (Bodaly et al. 1984). Prior to lake impoundment, there were significant differences in isozyme allele frequencies between various basins of SIL and between SIL and Issett Lake, at that time unconnected to SIL. After impoundment and river diversion through Issett Lake there were no significant differences among any of the SIL regions sampled or between SIL and Issett Lake. These changes in genetic stock structure of the study populations coincided with dramatic changes in the catch and grade of the SIL commercial fishery (Bodaly et al. 1984; see below).

The second case study concerns broad whitefish in the Mackenzie Delta (Tables 4, 5) (J. D. Reist, unpublished data). Results indicate considerable genetic differences between spawning aggregations for two of the three enzyme systems investigated in 1984 (Table 5; Fig. 6). Morphometric measurements agree with the genotypic data. Allele frequencies of LDH were marginally significantly different between 1983 and 1984 from the Peel River (Table 5), and

TABLE 4. Accumulated evidence for genetic stocks of fish in the Churchill and Mackenzie basins. The data types are vital statistics (vit stat), tag returns (tagging), meristic counts, parasite loads, morphology and genetic information. Species considered are lake whitefish (LWF), lake trout (LT), northern pike (NP), walleye (pickerel) (WP), goldeye (GE), inconnu (IN), unidentified cisco (CIS), and broad whitefish (BWF).

		Data from		Population		
Location	Species	Spawning	Type	Structure	Basis	Source
Churchill System						
Lac la Ronge	LWF	no	vit stat	yes	spatial	Qadri 1968
	LT	yes	vit stat	yes	spatial	Rawson 1961
	LT	yes	tagging	yes	spatial	"
	NP	no	meristic	yes	spatial	Koshinsky 1979
	WP	yes	tagging	yes	spatial	Rawson 1957a
Lakes upstream of Lac la Ronge (Montreal Lake, etc.)	WP	yes/no	genetic	yes	spatial	Clayton et al. 1974
Peter Pond Lake	LWF	no	parasite	yes	spatial	Rawson 1957b
Cree Lake	LWF	no	vit stat	?	spatial	Rawson 1959
Five lakes on the Churchill (Mountain Lake, etc.)	LWF	no	parasite	yes	spatial	Rawson 1960
Southern Indian Lake	WP	yes	tagging	yes	spatial	Bodaly 1980
	WP	yes	vit stat	yes	spatial	"
	WP	yes	morphology	yes	spatial	"
	LWF	no	morphology	yes	spatial	Bodaly et al. 1984 — see text
	LWF	no	parasite	yes	spatial	
	LWF	no	genetic	yes	spatial	"
Mackenzie System						
Lake Athabasca	LWF	no	morphology	yes	spatial	Rawson 1947
	LWF	no	vit stat	yes	spatial	"
	LWF	no	parasite	yes	spatial	"
Peace	GE	yes?	tagging	yes	spatial	Kristensen 1981
Athabasca Delta	GE	yes?	vit stat	yes	spatial	"
	GE	yes?	meristic	yes	spatial	"
Lake Athabasca vs Delta	WP	no?	vit stat	yes	spatial	Kristensen and Summers 1978
Great Slave Lake	LWF	no	vit stat	yes	spatial	Rawson 1947
	LWF	no	morphology	yes	spatial	Kennedy 1953
	LWF	no	parasite	yes	spatial	Moshenko and Low 1980
	LT	no	vit stat	yes	spatial	Kennedy 1954; Moshenko and Gillman 1983
	IN	no	parasite	yes	spatial	Fuller 1955
Great Bear Lake	LT	no	parasite	yes	spatial	Miller 1947; Miller and Kennedy 1948
	LT	no	vit stat	yes	spatial	Moshenko and Gillman 1983
	CIS	no	parasite	yes	spatial	Miller 1947
Mackenzie River (lower)	BWF	yes	genetic	yes	spatial	Reist, unpubl. data — see text
	BWF	yes	genetic	yes	temporal	
	BWF	yes	morphology	yes	spatial	"
	BWF	yes	meristic	no	spatial	"

TABLE 5. Numbers of alleles observed for broad whitefish in the lower Mackenzie River. White muscle extracts for B locus of glycerol-3-phosphate dehydrogenase (GPDH), B locus of lactate dehydrogenase (LDH), and locus, 3, 4 of malate dehydrogenase (MDH). SIG. is the *G*-test significance for the appropriate test and degrees of freedom.

	GPDH — B			LDH — B			MDH — 3, 4		
	a	b	c	a	b	d	1	2	3
1983									
Peel River	1	92	1	15	78	1	89	97	2
Ramparts	0	82	4	14	72	0	94	77	1
SIG.		ns			ns			ns	
1984									
Arctic Red River	0	120	0	8	112	0	116	122	2
Peel River	0	94	0	8	86	0	98	88	2
Mackenzie River	0	100	0	5	95	0	111	88	1
Travaillant River	0	102	0	25	77	0	142	62	0
SIG.		ns			$P<<0.005$			$P<<0.005$	
1983 vs 1984, Peel River									
SIG.		ns			$P<0.05$			ns	

rare alleles were absent in 1984, indicating the possibility of temporal structuring. The spatial limits to wide-ranging riverine stocks may be much more difficult to determine than lake-dwelling stocks.

Approaches to Stock Management

Three basic approaches to stock management have been utilized in the Mackenzie and Churchill basins: the use of yield indices and rules of thumb; test fishing and monitoring of population parameters; and the use of yield models. Yield indices (e.g. Ryder's (1965) morphoedaphic index) and rules of thumb (e.g. a commonly used rule is 0.5 pounds per acre (0.56 kg per ha)) are the only approaches used to determine allowable catches for small lake fisheries. Test fishing (before a fishery has begun) and the monitoring of populations (after a fishery is operational) to determine parameters such as growth, mortality, age at first maturity and catch per unit effort are commonly used techniques, but they are employed only for larger commercial fisheries. Population statistics are rarely gathered in enough detail for the application of any but the simplest fisheries yield models. The lack of attention to smaller commercial fisheries and to subsistence fisheries has probably resulted in the setting of many inappropriate quotas. Because many subsistence fisheries coexist with commercial fisheries, they do receive at least incidental attention.

In general, fish of the Mackenzie and Churchill basins grow relatively slowly and have low productivity, despite high standing crops of old, large individuals. The lake trout is typical. Fish older than 20 yr are common and some older than 50 yr are known in northern populations (Johnson 1976; Power 1978). Mortality and growth decrease noticeably after maturity is reached (Power 1978) and populations are often characterized by high standing crops of large, mature individuals (Johnson 1976; Power 1978). Lake trout populations also have a relatively poor capacity to compensate for the effects of exploitation. Healey (1978) noted that exploited lake trout populations with total mortality rates of greater than about 50 % declined and that although growth responded to exploitation, the lower limit for age at first maturity seemed to be fixed at 5–6 yr. The commercial lake trout fishery on Great Slave Lake may have collapsed because of the existence of only a small pool of immature fish which could have limited the ability of this species to respond quickly enough to increasing levels of exploitation (Healey 1978).

The lake sturgeon also is very sensitive to the effects of exploitation. This species can grow to >100 kg, and can live longer than 50 yr (Scott and Crossman 1973). The sturgeon was formerly quite abundant throughout the river channels and riverine lakes of the Churchill basin in Manitoba, but is now commercially extinct in the area, as it is in southern Manitoba (Harkness 1980). Rates of exploitation which were too high for population maintenance are the likely cause.

On the other hand, the lake whitefish has a greater ability to compensate for the effects of exploitation. The work of Healey (1975, 1980) has clearly demonstrated that growth, recruitment, and age at first maturity all respond to exploitation. Although little work has been conducted on other coregonid species in the two basins, responses are likely similar to the lake whitefish.

Examples

To illustrate many of the fisheries management problems in the Mackenzie and Churchill basins, brief descriptions of two contrasting types of fisheries will be presented. The fisheries are those at Great Slave Lake and Arctic Red River both in the NWT part of the Mackenzie basin. The Great Slave Lake fishery is a large, export commercial fishery. Domestic fishing also takes place on the lake but the magnitude of the subsistence catch is only sporadically estimated (see McCart and Den Beste (1979) for locations of domestic fisheries). Commercial fishing on the lake started in 1945 and expanded rapidly in the late 1940's and early 1950's (Bond 1974). Lake whitefish and lake trout have been the dominant species in commercial catches, averaging $\simeq 2.0\times10^6$ and $\simeq 1.2\times10^6$ kg, respectively, over the period 1948–57, with catches of both species declining by the late-1950's. Decreases in lake trout catches were most noticeable and were ascribed to over-exploitation (Keleher 1972; Bond 1974). The catch of both species was controlled by a pooled quota system, so lake trout catches were limited only to the amount of the total quota. Thus lake trout, which has higher value, was fished heavily in the early years of the fishery. Subsequently, a decision was made to manage the western basin of the lake solely for whitefish production, and the eastern basin was closed to commercial fishing to protect the lake trout population for sport and subsistence fishing (Moshenko and Low 1980).

Declines in the lake whitefish catch in Great Slave Lake were attributed partly to the exclusive use of gillnets of large mesh size (14.0 cm stretched mesh) which failed to elicit significant population responses to exploitation because only the larger, older fish were being removed (Healey 1975). Healey (1975) recommended that the mesh size for commercial fishing be reduced to 11.4 cm. In 1977, the mesh size was reduced to 13.3 cm and the population is being monitored to detect changes in growth, age at maturity, and catch per unit of effort (Moshenko and Low 1980). Studies on the genetic structure of the lake whitefish stocks in Great Slave Lake also are underway.

The Arctic Red River fishery, in contrast, is a small, river-based, mainly domestic fishery. In this fishery, catches are poorly known and the relationship between the fishery and the genetic stock structure of the species fished is not well understood. Arctic Red River is a predominantly native community located at the confluence of the Arctic Red and Mackenzie rivers, near the Mackenzie Delta (Fig. 2). There have been 3–12 commercial licence holders in the community over the period 1979–84. However, the total number of fishermen in the community is unknown because most participants fish domestically and do not require a licence. People who apply for commercial licences are those who wish to sell fish locally. Only licence holders are required to report catches annually. The Arctic Red River fishery operates mainly from late summer to early winter, and is directed at coregonids migrating upstream in fall and early winter for spawning. The broad whitefish is the primary species; lake whitefish, inconnu, and cisco also are caught. The reported commercial catch has varied from 700–6550 kg of broad whitefish (assuming 1 kg per fish) over the period 1979–84. However, in 1981, the total community harvest was estimated (by interview) to be 14 581 kg of broad whitefish (D. V. Gillman and A. H. Kristofferson, FWI, unpublished data). Jessop et al. (1974) estimated that 10 678 kg of broad whitefish were taken in the 1973 fishery (again assuming 1 kg per fish). The Arctic Red River fishery is probably exploiting more than one stock of broad whitefish. Broad whitefish and other coregonid species moving past the community of Arctic Red River could be stocks that spawn in the Arctic Red River itself or at any location upstream of Arctic Red River in the Mackenzie River proper. The stocks fished at Arctic Red River are probably fished at other locations so the stocks are exposed to multiple stresses. There has been little or no monitoring of population parameters for stocks exploited by this fishery.

Economic Considerations

The location of most of the commercial fisheries in the two basins in relation to existing transportation networks is a severe economic limiting factor (Thompson 1981; Gislason et al. 1982). Costs of transportation tend to be very high in relation to the value of the catch, especially if fish must be transported even short distances by air. Thompson (1981) found that the majority of 24 commercial fisheries in the NWT, Alberta, Saskatchewan, and Manitoba were economically marginal or unviable. Yields for many of the fisheries in the study area are well below their potential and catches are often determined more by effort than biological production (Bodaly 1986). Also, relatively unrestricted access to many of these fisheries has often attracted more labor and capital than is necessary to efficiently harvest available quotas (Cauvin 1979).

The technique of pulse, or rotational fishing, is being applied to some of the smaller fisheries in the two basins to attempt to alleviate some of the problems of reduced economic viability. Some lakes are harvested only once every 3–6 years, allowing for greater catches when harvesting does occur. However, this technique only lowers transportation and other harvest costs by a limited amount and the biological effects of intense, periodic harvests are not well understood (Wong and Whillans 1973; Reid and Momot 1985).

Environmental Impacts

The major environmental impacts in the Mackenzie basin are hydroelectric development, agriculture, forestry, mining, and oil and gas production (Rosenberg 1986). Agricultural and forestry activity occur only in the southern parts of the basin, whereas mining is scattered throughout the basin. Oil and gas production is centered around conventional reserves in Alberta and BC. Oil is extracted from beneath the Mackenzie River at Norman Wells, NWT. The indirect effects of energy reserve development include metal pollution from processing of hydrocarbons, acidic precipitation through emissions of tar sands processing plants in the Athabasca Valley, and influxes of people requiring new population centres, transportation facilities, sewage and water supplies (Rosenberg 1986).

Hydroelectric power production is the largest existing and potential economic use of water in the Mackenzie basin (MRBC 1981). At least eight dams exist in the Mackenzie basin, including those in the Lake Athabasca (2), Peace River (2) and Great Slave Lake (4) sub-basins. The Bennett and Peace Canyon dams on the Peace River are the largest, having a combine installed capacity of 3400 MW. Although the direct environmental effects of the Peace River hydroelectric facilities have been little studied (but see below for an account of the effects of hydroelectric development on the Churchill River), the downstream effects of flow regulation caused by the Bennett Dam have been well documented (see Rosenberg et al. 1987 for a more complete discussion). After dam closure, seasonal flooding of the Peace–Athabasca Delta no longer occurred, many lake basins within the delta began to dry out, and vegetational succession accelerated.

Four large hydroelectric developments with a total developed potential of about 8300 MW are in various stages of planning in the Mackenzie basin (Rosenberg 1986), and many more potential sites for dams and diversions exist throughout the basin (see fig. 6.1 of MRBC 1981; Day 1985). The regulation of Cordilleran flows below Great Slave Lake has the potential for severe environmental disruption, especially in the area of the Mackenzie Delta and estuary (Rosenberg 1986). Seasonal inputs of fresh water to the Mackenzie estuary may be crucial to the migration of coregonid fishes (Bond and Erickson 1985). Spring flooding in the Mackenzie Delta maintains the timing of ice break-up, controls vegetation succession, and maintains channel morphologies (Gill 1973; Kellerhals and Gill 1973).

Major undeveloped reserves of conventional oil and gas are located in the Mackenzie Delta and Beaufort Sea, and pipelines have been proposed to bring these frontier reserves to southern markets. The ecological effects of accidental oil spills on lower trophic levels in aquatic systems in the Mackenzie basin are reviewed by Rosenberg (1986). Non-conventional reserves in the upper Mackenzie basin (tar sands and heavy oils) are estimated to amount to 1.1×10^{11} m^3 although only 10–20 % of this amount may be recoverable.

The major natural resource activities in the Churchill basin are mining and hydroelectric development. As in the Mackenzie basin, mining activity is scattered throughout the Churchill basin (CRS 1976; Wright 1980). Although a number of smaller hydroelectric projects exist in the Churchill basin, the Churchill River diversion has been the major environmental perturbation. This project rerouted 760 $m^3 \cdot s^{-1}$ from the Churchill basin into the Nelson basin to augment flows for power plant operation in the lower Nelson (Newbury et al. 1984). The effects of this diversion are described by Newbury et al. (1984) and Hecky et al. (1984). Lakes along the lower Churchill below Southern Indian Lake have been dewatered, whereas lakes along the diversion route have been subjected to flows that are 10 times normal. Impoundment of Southern Indian Lake (SIL) caused extensive shoreline erosion and significant increases in suspended sediment levels. The contamination of fish by mercury as a result of impoundment threatened a major domestic food source and the marketability of predatory fish.

The commercial whitefish fishery on SIL collapsed following lake impoundment and river diversion. Within 4 yr of SIL impoundment, the catch per unit of effort in the whitefish fishery had fallen to about 1/2 of its pre-impoundment mean value (Bodaly et al. 1984). The quota for the fishery was not adjusted downward and fihsermen maintained the total catch by increasing effort and fishing a basin of the lake formerly avoided because of lower grade catches. Within 6 yr after impoundment, the total catch had fallen to 1/5 pre-impoundment levels and had not recovered by 4 yr after that. Initial declines in catch per effort apparently were due to the effects of lake impoundment and the outmigration of fish over the control dam at the natural lake outlet and through the diversion channel. Failure to adjust quotas in the face of environmental impacts probably contributed to the collapse of the fishery.

Conclusions

The Churchill and Mackenzie basins are areas of low productivity, short growing seasons, and low levels of dissolved nutrients. Primary production by phytoplankton and macrophytes is often an order of magnitude lower than in temperate and tropical systems. For example, in the Plata basin, South America, phytoplankton production averages about 200 g $C \cdot m^{-2} \cdot yr^{-1}$ whereas macrophyte production ranges from about 200 to 500 g $C \cdot m^{-2} \cdot yr^{-1}$ (Quiros and Cuch 1989). In the Hudson, phytoplankton production ranges from 170 to 800 g $C \cdot m^{-2} \cdot yr^{-1}$ (Limburg et al. 1989). Phytoplankton production in the Churchill and Mackenzie basins ranges from >4 to 80 g $C \cdot m^{-2} \cdot yr^{-1}$ whereas macrophyte production ranges up to 30 g $C \cdot m^{-2} \cdot yr^{-1}$. These low rates of primary production must translate into low rates of fish production, although little is known of fish production in the two basins. In contrast with the low rates of production, standing crops of old, large fish can be quite high because of slow growth, low mortality, and because fish concentrate during migrations. In addition, many of the species being fished are highly susceptible to the effects of exploitation.

Despite the major differences in climate and productivity, the fisheries of the Mackenzie and Churchill basins share many characteristics with those in tropical areas. In northern Canada much of the fisheries production is for local sale and domestic use. Commercial fishing, for sale outside the area, and sport fishing do not dominate in many parts of the two basins largely because of high transportation costs. Likewise, in most river basins in tropical developing countries, fisheries tend to be traditional enterprises, mainly supplying local areas (e.g. the Niger: Malvestuto and Meredith 1989; the Orinoco: Novoa 1989; and the Gambia: Lesack 1986). In contrast, the fisheries of temperate systems, located in developed countries, usually have a highly developed commercial industry with sport fisheries becoming increasingly important in recent times (e.g. the Fraser: Northcote and Larkin 1989; the Columbia: Ebel et al. 1989; and the Danube: Bacalbasa-Dobrovici 1989).

The degree and type of environmental impacts in the Mackenzie and Churchill basins also are similar to impacts in river basins in tropical developing countries. Major impacts have often been associated with resource extraction, such as mining, oil and gas developments, and timber removal, rather than with the effects of industrial developments such as manufacturing and chemical industries. Northern Canadian rivers have been the object of increasing hydroelectric power development (Rosenberg et al. 1987) and this is also the case for many tropical rivers (e.g. the Niger: Malvestuto and Meredith 1989; the Orinoco: Novoa 1989; and the Gambia: Lesack 1986). Arctic and subarctic rivers, because of low productivity and low species diversity may, however, be less resilient to impacts of human origin than temperate or tropical systems. Large-scale disruptions of fish habitat caused by major hydroelectric projects in the Churchill basin and other northern Canadian basins (Rosenberg et al. 1987) are likely to apply to the huge Mackenzie basin in the future.

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References

Atton, F. M., and J. J. Merkowsky. 1983. Atlas of Saskatchewan fish. Sask. Parks Renew. Resour. Fish. Tech. Rep. 83-2: 281 p.

Bacalbaşa-Dobrovici, N. 1989. The Danube and its fisheries, p. 455-468. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Bodaly, R. A. 1980. Pre- and post-spawning movements of walleye, *Stizostedion vitreum*, in Southern Indian Lake, Manitoba. Can. Tech. Rep. Fish. Aquat. Sci. 931: v + 30 p.

1986. Biology, exploitation and culture of coregonid fishes in Canada, Arch. Hydrobiol. Beih. 22: 1-30.

Bodaly, R. A., T. W. D. Johnson, R. J. P. Fudge, and J. W. Clayton. 1984. Collapse of the lake whitefish (*Coregonus clupeaformis*) fishery in Southern Indian Lake, Manitoba, following lake impoundment and river diversion. Can. J. Fish. Aquat. Sci. 41: 692–700.

Bond, W. A. 1974. The Great Slave Lake commercial fishery. 1973. Fish. Mar. Serv. Tech. Rep. Ser. CEN/T-74-8: 38 p.

1980. Fishery resources of the Athabasca River downstream of Fort McMurray, Alberta: Volume I. Alberta Oil Sands Environmental Research Program, Rep. 89 (AOSERP AF-4-3-2): 81 p.

1982. A study of the fishery resources of Tuktoyaktuk Harbour, southern Beaufort Sea coast, with special reference to life histories of anadromous coregonids. Can. Tech. Rep. Fish. Aquat. Sci. 1119: vii + 90 p.

Bond, W. A., and R. N. Erickson. 1982. Preliminary results of a fisheries study of two freshwater lake systems on the Tuktoyaktuk Peninsula, Northwest Territories. Can. Data Rep. Fish. Aquat. Sci. 348: vi + 52 p.

1985. Life history studies of anadromous coregonid fishes in two freshwater lake systems on the Tuktoyaktuk Peninsula, Northwest Territories. Can. Tech. Rep. Fish. Aquat. Sci. 1336: vii + 61 p.

Brunskill, G. J. 1986. Environmental features of the Mackenzie system, p. 435–471. *In* B. R. Davies and K. F. Walker [ed.] The ecology of river systems. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Cauvin, D. M. 1979. Regulating access in Canada's inland fisheries. J. Fish. Res. Board Can. 36: 827–836.

Chang-Kue, K. T. J., and E. F. Jessop. 1983. Tracking the movements of adult broad whitefish (*Coregonus nasus*) to their spawning grounds in the Mackenzie River, Northwest Territories, p. 248–266. *In* D. G. Pincock [ed.] Proceedings of Fourth International Conference on Wildlife Biotelemetry, Halifax, NS.

CRS (Churchill River Study). 1976. Synthesis. Tech. Rep. Sask. Dep. Environ., Regina, SK. 215 p.

Clayton, J. W., R. E. K. Harris, and D. N. Tretiak. 1973. Geographical distribution of alleles for supernatant malate dehydrogenase in walleye (*Stizostedion vitreum vitreum*) populations from western Canada. J. Fish. Res. Board Can. 31: 342–345.

Cleugh, T. R. 1974. The hydrography of Southern Indian Lake: present conditions and implications of hydroelectric development. Lake Winnipeg, Churchill and Nelson Rivers Study Board, 1971–1975. Tech. Rep. Appen. 5, Vol. 1, Rep. C: 195 p.

Crossman, E. J., and D. E. McAllister. 1986. Zoogeography of freshwater fishes of the Hudson Bay drainage, Ungava Bay and the Arctic Archipelago, p. 53–104. *In* C. H. Hocutt and E. O. Wiley [ed.] The zoogeography of North American freshwater fishes. John Wiley and Sons, New York.

Davis, E. 1976. Churchill River study (Missinipe probe). Water Quality. Final Rep. 31. Dep. Environ., Regina, SK. 62 p.

Day, J. C. 1985. Canadian interbasin diversions. Inquiry on federal water policy. Research Paper 6. Environ. Canada, Ottawa, ON. 111 p.

Dean, E. L. 1980. Highrock Lake fisheries survey. Sask. Fish. Lab., Dep. Tourism Renew. Resour. Rep. 80-2: 83 p.

Dietz, K. G. 1973. The life history of walleye (*Stizostedion vitreum vitreum*) in the Peace–Athabasca Delta. Alberta Dep. Lands and Forests, Fish and Wildl. Div. 52 p.

Donald, D. B., and A. H. Kooyman. 1977. Migration and population dynamics of the Peace–Athabasca Delta goldeye population. Can. Wildl. Serv. Occas. Pap. 31: 21 p.

Dymond, J. R. 1933. Biological and oceanographic conditions in Hudson Bay. 8. The coregonine fishes of Hudson and James Bay. Contrib. Can. Biol. Fish. 8: 1–12.

Ebel, W. J., C. D. Becker, J. W. Mullan, and H. L. Raymond. 1989. The Columbia River — towards a holistic understanding, p. 205-219. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Fee, E. J., M. P. Stainton, and H. J. Kling. 1985. Primary production and related limnological data for some lakes of the Yellowknife, NWT area. Can. Tech. Rep. Fish. Aquat. Sci. 1409: v + 55 p.

Fuller, W. A. 1955. The inconnu (*Stenodus leucichthys mackenziei*) in Great Slave Lake and adjoining waters. J. Fish. Res. Board Can. 12: 768–780.

Gallaway, B. J., W. B. Griffiths, P. C. Craig, W. J. Gazey, and J. W. Helmricks. 1983. An assessment of the Colville River delta stock of Arctic cisco — migrants from Canada? Biol. Pap. Univ. Alaska 21: 4–23.

Gill, D. 1973. Modification of northern alluvial habitats by river development. Can. Geogr. 17: 138–153.

Gislason, G. S., J. A. MacMillan, and J. W. Craven. 1982. The Manitoba commercial freshwater fishery: an economic analysis. Univ. Manitoba Press, Winnipeg, MB. 311 p.

Harkness, W. J. K. 1980. Report on the sturgeon situation in Manitoba. Man. Dep. Nat. Res. MS Rep. 80-3: 18 p.

Hatfield, C. T., J. N. Stein, M. R. Falk, and C. S. Jessop. 1972. Fish resources of the Mackenzie River valley. Interim Rep. 1, Vol. 1. Fish. Serv., Environ. Can., Winnipeg, MB. 247 p.

Healey, F. P., and L. L. Hendzel. 1980. Physiological indicators of nutrient deficiency in lake phytoplankton. Can. J. Fish. Aquat. Sci. 37: 442–453.

Healey, M. C. 1975. Dynamics of exploited whitefish populations and their management with special reference to the Northwest Territories. J. Fish. Res. Board Can. 32: 427–448.

1978. The dynamics of exploited lake trout populations and implications for management. J. Wildl. Manage. 42: 307–328.

1980. Growth and recruitment in experimentally exploited lake whitefish (*Coregonus clupeaformis*) populations. Can. J. Fish. Aquat. Sci. 37: 255–267.

Hecky, R. E., and S. J. Guildford. 1984. Primary productivity of Southern Indian Lake before, during, and after impoundment and Churchill River diversion. Can. J. Fish. Aquat. Sci. 41: 591–604.

Hecky, R. E., R. W. Newbury, R. A. Bodaly, K. Patalas, and D. M. Rosenberg. 1984. Environmental impact prediction and assessment: the Southern Indian Lake experience. Can. J. Fish. Aquat. Sci. 41: 720–732.

Jessop, C. S., K. T. J. Chang-Kue, J. W. Lilley, and R. J. Percy. 1974. A further evaluation of the fish resources of the Mackenzie River valley as related to pipeline development. Task Force on Northern Oil Development, Environmental–Social Committee, Northern Pipelines, Rep. 74-7. Info. Can. Cat. No. R72-13674 QS-1555-000-EE-A1: 95 p.

JOHNSON, L. 1976. Ecology of arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, Arctic char, *S. alpinus*, and associated species in unexploited lakes of the Canadian Northwest Territories. J. Fish. Res. Board Can. 33: 2459-2488.

KELEHER, J. J. 1972. Great Slave Lake: effects of exploitation on the salmonid community. J. Fish. Res. Board Can. 29: 741-753.

KELLERHALS, R., AND D. GILL. 1973. Observed and potential downstream effects of large storage projects in northern Canada, p. 731-754. *In* Onzieme Congres des Grands Barrages. Commission Internationale des Grands Barrages, Madrid, 1973.

KENNEDY, W. A. 1953. Growth, maturity, fecundity and mortality in the relatively unexploited whitefish, *Coregonus clupeaformis*, of Great Slave Lake. J. Fish. Res. Board Can. 10: 413-441.

1954. Growth, maturity and mortality in the relatively unexploited lake trout, *Cristivomer namaycush*, of Great Slave Lake. J. Fish. Res. Board Can. 11: 827-852.

KOSHINSKY, G. D. 1965. Limnology and fisheries of five Precambrian headwater lakes near Lac la Ronge, Saskatchewan. Sask. Dep. Nat. Resour. Fish. Rep. 7: 52 p.

1968. The limnology and fisheries of 28 small lakes situated on the Precambrian Shield near Lac la Ronge, Saskatchewan, 1960-1967. Part II. Descriptions of individual lakes. Sask. Fish. Lab., Saskatoon, SK. 212 p.

1979. Northern pike, Lac la Ronge, parts 1 and 2. Sask. Dep. Tourism Renew. Resour. Fish. Tech. Rep. 79-8: 303 p. (cited by permission).

KRISTENSEN, J. 1979. Walleye studies in the Peace-Athabasca Delta, 1978. Prepared for Fisheries Subcommittee Peace-Athabasca Delta Monitoring Committee by LGL Limited, Edmonton, AB. 54 p.

1980. The need for adequate fish passage facilities in the Peace-Athabasca Delta — a synopsis. A report to Alberta Environment. Special Projects. 9 p.

1981. Investigations of goldeye and other fish species in the Wood Buffalo National Park section of the Peace-Athabasca Delta, 1977. Can. MS Rep. Fish. Aquat. Sci. 1560: v + 64 p.

KRISTENSEN, J., AND S. A. SUMMERS. 1978. Fish populations in the Peace-Athabasca Delta and the effects of water control structures on fish movements. Can. Fish. Mar. Serv. MS Rep. 1465: 62 p.

LAWRENCE, M. J., G. LACHO, AND S. DAVIES. 1984. A survey of the coastal fishes of the southeastern Beaufort Sea. Can. Tech. Rep. Fish. Aquat. Sci. 1220: x + 178 p.

LESACK, L. F. W. 1986. Estimates of catch and potential yield for the riverine artisanal fishery in The Gambia, West Africa. J. Fish. Biol. 28: 679-700.

LIMBURG, K. E., S. A. LEVIN, AND R. E. BRANDT. 1989. Perspectives on management of the Hudson River ecosystem, p. 265-291. *In* D. P. Dodge [ed.] Proceedings of the International Large Rivers Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

LINDSEY, C. C., AND J. D. MCPHAIL. 1986. Zoogeography of fishes of the Yukon and Mackenzie basins, p. 639-674. *In* C. H. Hocutt and E. O. Wiley [ed.] The zoogeography of North American freshwater fishes. John Wiley and Sons, New York.

LIVINGSTONE, D. A., M. ROWLAND, AND P. E. BAILEY. 1982. On the size of African riverine fish faunas. Am. Zool. 22: 361-369.

LOWER, A. R. M. 1915. A report on the fish and fisheries of the west coast of James Bay. App. Ann. Rep. Dep. Naval Ser. Can. 1914: 3-28.

MALVESTUTO, S. P., AND E. K. MEREDITH. 1989. Assessment of the Niger River fishery in Niger (1983-1985) with implications for management, p. 533-544. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

MCCART, P. J. 1982. An assessment of the fisheries resources of the Great Bear and Mackenzie rivers in the vicinity of proposed IPL pipeline crossings. Prepared for the Inter Provincial Pipelines Ltd. by Aquatic Environments Limited, Calgary, AB. 33 p.

1986. Fish and fisheries of the Mackenzie system, p. 493-515. *In* B. R. Davies and K. F. Walker [ed.] The ecology of river systems. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

MCCART, P. J., AND J. DEN BESTE. 1979. Aquatic resources of the Northwest Territories. Prepared for Science Advisory Board of the Northwest Territories by Aquatic Environments Limited, Calgary, AB. 54 p.

MCCART, P. J., D. TRIPP, AND R. WITHLER. 1982. Spawning and distribution of lake whitefish (*Coregonus clupeaformis*) in Athabasca River and Lake Athabasca. Prepared for Alberta Environment, Edmonton, AB, by Aquatic Environments Limited, Calgary, AB. 38 p.

MCLEOD, C. L., AND J. P. O'NEIL. 1983. Major range extensions of anadromous salmonids and first record of chinook salmon in the Mackenzie River drainage. Can. J. Zool. 61: 2183-2184.

MILLER, R. B. 1947. Great Bear Lake. *In* Northwest Canadian fisheries surveys in 1944-1945. Bull. Fish. Res. Board Can. 72: 94 p.

MILLER, R. B., AND W. A. KENNEDY. 1948. Observations on the lake trout of Great Bear Lake. J. Fish. Res. Board Can. 7: 176-189.

MORIN, R., J. J. DODSON, AND G. POWER. 1981. The migrations of anadromous cisco (*Coregonus artedii*) and lake whitefish (*C. clupeaformis*) in estuaries of eastern James Bay. Can. J. Zool. 59: 1600-1607.

MOSHENKO, R. W., AND D. V. GILLMAN. 1983. Creel census and biological data from the lake trout sport fishery on Great Bear and Great Slave lakes, Northwest Territories, 1977-78. Can. Data Rep. Fish. Aquat. Sci. 389: vi + 73 p.

MOSHENKO, R. W., AND G. LOW. 1980. Data from the commercial fishery for lake whitefish, *Coregonus clupeaformis* (Mitchill), on Great Slave Lake, Northwest Territories, 1979. Can. Data Rep. Fish. Aquat. Sci. 194: v + 29 p.

MRBC (Mackenzie River Basin Committee). 1981. Mackenzie River basin study report. A report under the 1978-81 Federal-Provincial Study Agreement respecting the water and related resources of the Mackenzie River basin. Environ. Can., Inland Waters Directorate, Regina, SK. ISBN

NEWBURY, R. W., G. K. MCCULLOUGH, AND R. E. HECKY. 1984. The Southern Indian Lake impoundment and Churchill River diversion. Can. J. Fish. Aquat. Sci. 41: 548-557.

NORTHCOTE, T. G., AND P. A. LARKIN. 1989. The Fraser: a major salmonine production system, p. 172-204. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

NOVOA, D. F. 1989. The multispecies fisheries of the Orinoco River, development, present status and management strategies, p. 422-428. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

OGLESBY, R. T. 1977. Relationships of fish yield to lake phytoplankton standing crop, production, and morphoedaphic factors. J. Fish. Res. Board Can. 34: 2271–2279.

OTT, B. S., AND A. D. SEKERAK. 1976. Walleye investigations, p. 1–36. *In* J. Kristensen, B. S. Ott, and A. D. Sekerak [ed.] Walleye and goldeye fisheries investigations in the Peace–Athabasca Delta — 1975. Part I. Prepared for Alberta Oil Sands Environmental Research Program by LGL Limited. AOSERP Rep. 2: 103 p.

POWER, G. 1978. Fish population structure in arctic lakes. J. Fish. Res. Board Can. 35: 53–59.

PREST, V. K. 1970. Quaternary geology of Canada, p. 676–764. *In* R. J. W. Douglas [ed.] Geology and economic minerals of Canada. Geol. Surv. Can. Econ. Geol. Rep. 1.

QADRI, S. U. 1968. Growth and reproduction of the lake whitefish, *Coregonus clupeaformis*, in Lac la Ronge, Saskatchewan. J. Fish. Res. Board Can. 25: 2091–2100.

QUIROS, R., AND S. CUCH. 1989. The fishery of the lower Plata River basin: fish harvest and limnology, p. 429–443. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

RAWSON, D. S. 1957a. The life history and ecology of the yellow walleye, *Stizostedion vitreum*, in Lac la Ronge, Saskatchewan. Trans. Am. Fish. Soc. 86: 15–36.

1957b. Limnology and fisheries of five lakes in the upper Churchill drainage, Saskatchewan. Sask. Dep. Nat. Resour. Fish. Rep. 3: 61 p.

1959. Limnology and fisheries of Cree and Wollaston lakes in northern Saskatchewan. Sask. Dep. Nat. Resour. Fish. Rep. 4: 73 p.

1960. Five lakes on the Churchill River near Stanley, Saskatchewan. Sask. Dep. Nat. Resour. Fish. Rep. 5: 38 p.

1961. The lake trout of Lac la Ronge, Saskatchewan. J. Fish. Res. Board Can. 18: 423–462.

REID, D. M., AND W. T. MOMOT. 1985. Evaluation of pulse fishing for the walleye, *Stizostedion vitreum vitreum*, in Henderson Lake, Ontario. J. Fish. Biol. 27 (Suppl. A): 235–251.

ROSENBERG, D. M. 1986. Resources and development of the Mackenzie system, p. 517–540. *In* B. R. Davies and K. F. Walker [ed.] The ecology of river systems. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

ROSENBERG, D. M., AND D. R. BARTON. 1986. The Mackenzie River system, p.425–433. *In* B. R. Davies and K. F. Walker [ed.] The ecology of river systems. Dr W Junk Publishers, Dordrecht, The Netherlands.

ROSENBERG, D. M., R. A. BODALY, R. E. HECKY, AND R. W. NEWBURY. 1987. The environmental assessment of hydroelectric impoundments and diversions in Canada, p. 71–104. *In* M. C. Healey and R. R. Wallace [ed.] Canadian aquatic resources. Can. Bull. Fish. Aquat. Sci. 215.

RYDER, R. A. 1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. 94: 214–218.

SCHINDLER, D. W. 1972. Production of phytoplankton and zooplankton in Canadian Shield lakes, p. 311–332. *In* Z. Kajak and A. Hillbricht-Ilkowska [ed.] Proceedings of the IBP-UNESCO Symposium of Productivity Problems of Freshwaters, Warszawa-Krakow.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 194: 966 p.

STEIN, J. N., C. S. JESSOP, T. R. PORTER, AND K. T. J. CHANG-KUE. 1973. Fish resources of the Mackenzie River valley. Interim Rep. II. Dep. Environ., Fish. Serv., Winnipeg, MB. 260 p.

SUMMERS, S. A. 1978. Walleye studies in Richardson Lake and Lake Athabasca, April-July 1977. Prepared for Fisheries Subcommittee Peace–Athabasca Delta Monitoring Committee by LGL Limited, Edmonton, AB. 70 p.

THOMPSON, P. C. 1981. The economic performance of the commercial skiff fishery in western Canada. Can. Tech. Rep. Fish. Aquat. Sci. 1037: 21 p.

TRIPP, D. B., AND P. J. MCCART. 1979. Investigations of the spring spawning fish populations in the Athabasca and Clearwater rivers upstream from Fort McMurray. Vol. 1. Prepared for Alberta Oil Sands Environmental Research Program by Aquatic Environments Limited, Calgary, AB. AOSERP Project WS 1.6.1: 27 p.

TRIPP, D. B., P. J. MCCART, R. D. SAUNDERS, AND G. W. HUGHES. 1981. Fisheries studies in the Slave River delta, N.W.T. Final report. *In* Mackenzie River Basin Study, Suppl. 6. Prepared for Joint Federal–Provincial Mackenzie River Basin Committee. 262 p.

WALKER, S. J. 1931. Investigations at Churchill, Manitoba. Contrib. Can. Biol. Fish. (N.S.) 6: 472–474.

WELCOMME, R. L. 1985. River fisheries. FAO Fish. Tech. Pap. 262: 330 p.

WONG, B., AND T. WHILLANS. 1973. Limnological and biological survey of Hottah Lake, Northwest Territories. Fish. Mar. Serv. Tech. Rep. Ser. CEN/T-73-6: 69 p.

WRIGHT, D. G. 1980. A twenty-five year scenario of anticipated developments that may have an impact on fish and fish habitat in the prairie provinces and the Northwest Territories. Can. Fish. Mar. Serv. MS Rep. 1546: iv + 31 p.

Fisheries and Yields in the Moose River Basin, Ontario

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Abstract

BROUSSEAU, C. S., AND G. A. GOODCHILD. 1989. Fisheries and yields in the Moose River Basin, Ontario, p. 145–158. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

A review of the major tributaries in the Moose River basin, Ontario, including major stresses affecting the fisheries, and estimates of fish yields, is presented. The Moose River basin (109 000 km^2) consists of several large rivers that flow into the 106 km long Moose River, tributary to James Bay. The tributaries vary in length from 215 to 491 km with mean basal flows ranging from 32 to 780 $m^3 \cdot s^{-1}$ in the Moose River mainstream. The major sport fish species in the rivers are walleye, northern pike and lake sturgeon. The basin has been developed only since the turn of the century and the major impacts on the fishery have been hydroelectric generation, the pulp and paper industry and sport and commercial fisheries. These developments have depressed fish populations and disrupted fish habitat at several locations in the basin. Fish yields are low with standing stock estimates on the Frederick House River of 47.6 $kg \cdot ha^{-1}$, a total yield of 11.4 $kg \cdot ha^{-1}$ and a p/b ratio of only 0.24. Management strategies aimed at protecting the broodstock such as maximum size limits, protected slot size limits, and water level management agreements, are crucial to the maintenance of viable fish populations in this northern environment.

Résumé

BROUSSEAU, C. S., AND G. A. GOODCHILD. 1989. Fisheries and yields in the Moose River Basin, Ontario, p. 145–158. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Les auteurs traitent des principaux tributaires de la rivière Moose, en Ontario, des principales contraintes y affectant les pêches et des rendements estimés en poisson. Le bassin de la rivière Moose (109 000 km^2 comprend plusieurs cours d'eau importants qui se déversent tout au long des 106 km de la Moose, un important tributaire de la baie James. La longueur de ces tributaires varie de 215 à 491 km et leur débit de base de 32 à 780 $m^3 \cdot s^{-1}$. Les principales espèces sportives de la rivière Moose sont le doré jaune, le grand brochet et l'esturgeon de lac. La mise en valeur de ce bassin ne remonte qu'au début du siècle et la production hydro-électrique, l'industrie des pâtes et papiers et les pêches sportive et commerciale sont les principaux facteurs ayant influé sur les ressources halieutiques. Ces activités ont eu pour effet de réduire les populations de poisson et d'en perturber l'habitat en plusieurs points du bassin. Les rendements piscicoles sont faibles. Ainsi, les stocks estimés de la rivière Frederick House sont de 47,6 $kg \cdot ha^{-1}$ pour un rendement total de 11,4 $kg \cdot ha^{-1}$ et un rapport p/b de seulement 0,24. L'application de stratégies de gestion visant à protéger les stocks de géniteurs, notamment par l'imposition de tailles limites maximales et de gammes de tailles et par la conclusion d'ententes pour le maintien du niveau des eaux, s'avère essentielle pour le maintien de populations de poisson viables dans ce milieu septentrional.

Introduction

Information on fisheries of large rivers in northern Ontario is sparse, relative to that available on lakes (Ryder and Pesendorfer 1989). A few reports, however, focus on particular sites in the Moose River Basin (Stanfield et al. 1972; MacRitchie 1981), but none examine the river system as a whole. Recently, inventory surveys and preliminary yield estimates were initiated since little was known about the capability of fisheries in the rivers to withstand development, especially to meet increasing demands for energy production, flood control and waste assimilation.

This paper reviews biological, chemical and physical data of the Moose River, a tributary to James Bay. The major stresses on the fishery, and standing stocks and yield estimates are described.

History

The first known inhabitants in the Moose River basin were the Shield Archaic Peoples (5000 B.P.) followed by the Laurel Peoples (2000 B.P.). Both groups subsisted on fish and game in the rivers and surrounding terrain. From 800 AD to the present, the area has been occupied by Cree and Ojibway Indians (OMNR 1983).

Until the late 1790's, native Indians were only sparsely settled in the area. Documents dating back to 1610 (OMNR 1985a) describe the importance of the Moose–Missinaibi River valley and the tributary Mattagami River system as major fur trading routes leading to the island village of Moose Factory at the mouth of the river where it enters James Bay. This was the most important fur trading post in northern Ontario before the twentieth century.

In 1900, the Ontario Government made its first official exploration of the area to determine the resource potential for Northern Ontario. In 1905, gold was discovered in the basin about 80 km east of Timmins and by 1909, the needs of the new mining communities provided the stimulus for rail and power development as well as an agricultural and forest industry. By 1920, a railway transected the Moose River basin and by 1931, the Ontario Northland Railway reached its terminus at the town of Moosonee (OMNR 1985a), on the mainland opposite Moose Factory.

Power needs of mining communities initiated the development of several dams on the Mattagami River. Sandy Falls dam was constructed in 1910 and a dam at Wawaitin Falls was completed in 1912. In 1933, transmission lines were constructed to transmit additional power from the Abitibi River, and by 1927, other dams were constructed on the Mattagami River to supply power to a pulp and paper mill at Kapuskasing. In all, 15 power dams and 19 control dams have been constructed on the rivers since the early 1900's, with the last major dams being constructed in the 1960's. The installed turbine capacity of the dams is about 1 000 MW. Presently, several dams on the Mattagami River are being expanded to increase power capacity.

The Abitibi and Mattagami river systems have received the majority of the development in order to supply electricity to mining and pulp and paper communities. Dams have created several flooded reservoirs which have dramatically changed the original nature of the rivers. Some rivers have also been used for the transportation of pulpwood to mills.

Another major tributary of the Moose River is the Missinaibi River. Ontario Hydro has identified three sites with significant hydroelectric power potential.

Basin Description

Morphometry

The Moose River basin drains approximately 109 000 km^2, of which about 9 000 km^2 lies in the Province of Quebec (Fig. 1). The 106 km long Moose River originates at the junction of the Missinaibi and Mattagami rivers and runs north–northeast into James Bay. Physical characteristics of the Moose River and its major tributaries are shown in Table 1. The annual flow regimes for the rivers in the basin are similar to those on the Nottaway River on the east side of James Bay (Roy 1989).

The Moose River basin extends over the Precambrian Shield in the south and the Hudson Bay Lowland in the north. The elevation of the boundary between the Lowland and the adjoining Shield is approximately 152 m above sea level. The Shield is comprised of ancient crystalline granites interspersed with meta-sediments and meta-volcanic rocks. Bedrock outcrops are common, often punctuating the rivers to form rapids and falls. In the southeastern portion of the basin, unconsolidated lacustrine sediments were deposited by the ancient Pleistocene lake, Barlow–Ojibway, in an area now known as the clay belt (McCrea and Merriman 1981).

The Lowland is composed of marine, fluvial and glacial-till deposits, overlain by peat with combined depths up to 200 m. Poor drainage results in wet terrain with extensive bogs and fens in the south and peat plateaus in the north. On the river bank levees, where better drainage exists, there are narrow belts of white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and white birch (*Betula papyrifera*) stands. Beyond and parallel to these is a zone of largely pure black spruce (*Picea mariana*) approximately 100–300 m from the river bank. These trees are small, often less than 2 m in height, and within 300–500 m of the river, scrub-type trees are predominant but eventually give way to open muskeg (Stanfield et al. 1972).

Channels in the basin are normally well defined with narrow flood plains. Banks rise 5–15 m above the mid-summer water level forming abrupt levees. Rivers are generally shallow and slow moving with a highly seasonal flow regime (McCrea et al. 1984). The gradient on the Shield is about 1.0–1.5 $m \cdot km^{-1}$ and on the Lowland only 0.5–1.0 $m \cdot km^{-1}$. Tidal movements have been observed upstream of the mouth of the Moose River as far as about 30 km, while the maximum variability of tidal height at the mouth is about 3 m (McCrea and Merriman 1981).

The Moose River consists of complex pattern of bars and islands with braiding from 0 to 65 %. In lower reaches there is some anastomosis. Each tributary possesses its own characteristics but generally has a low degree of sinuosity in the lower reaches (1.0–1.05), increasing up to 1.5 in the upper reaches. Sinuosity is generally single phased, consisting of equidistant channels that are incised in the upper reaches only. The substrate is composed of approximately 25 % rubble, 60 % sand, 10 % boulder, and 5 % organic muck.

Climate

The Moose River basin is characterized by a modified continental climate influenced by Hudson and James Bay to the north and the Laurentian Great Lakes to the south. Temperature and precipitation information at the mouth of the Moose River is in Table 2.

Lakes freeze in mid-October in the north to early November in the south. Rivers tend to freeze ten to twenty days later. Spring break-up is the beginning of maximum run-off, usually in late April to early May. As break-up progresses, floating ice drifts downstream and frequently forms ice jams that block drainage and produce flooding. The rivers do not generate the large amounts of frazil ice that occur on the east side of James Bay (Roy 1989). Off the mouth of the Moose River, sea ice break-up occurs near the end of June but floating pack ice persists until early August (OMNR 1985a).

Water Chemistry

Water chemistry for the major rivers in the Moose River

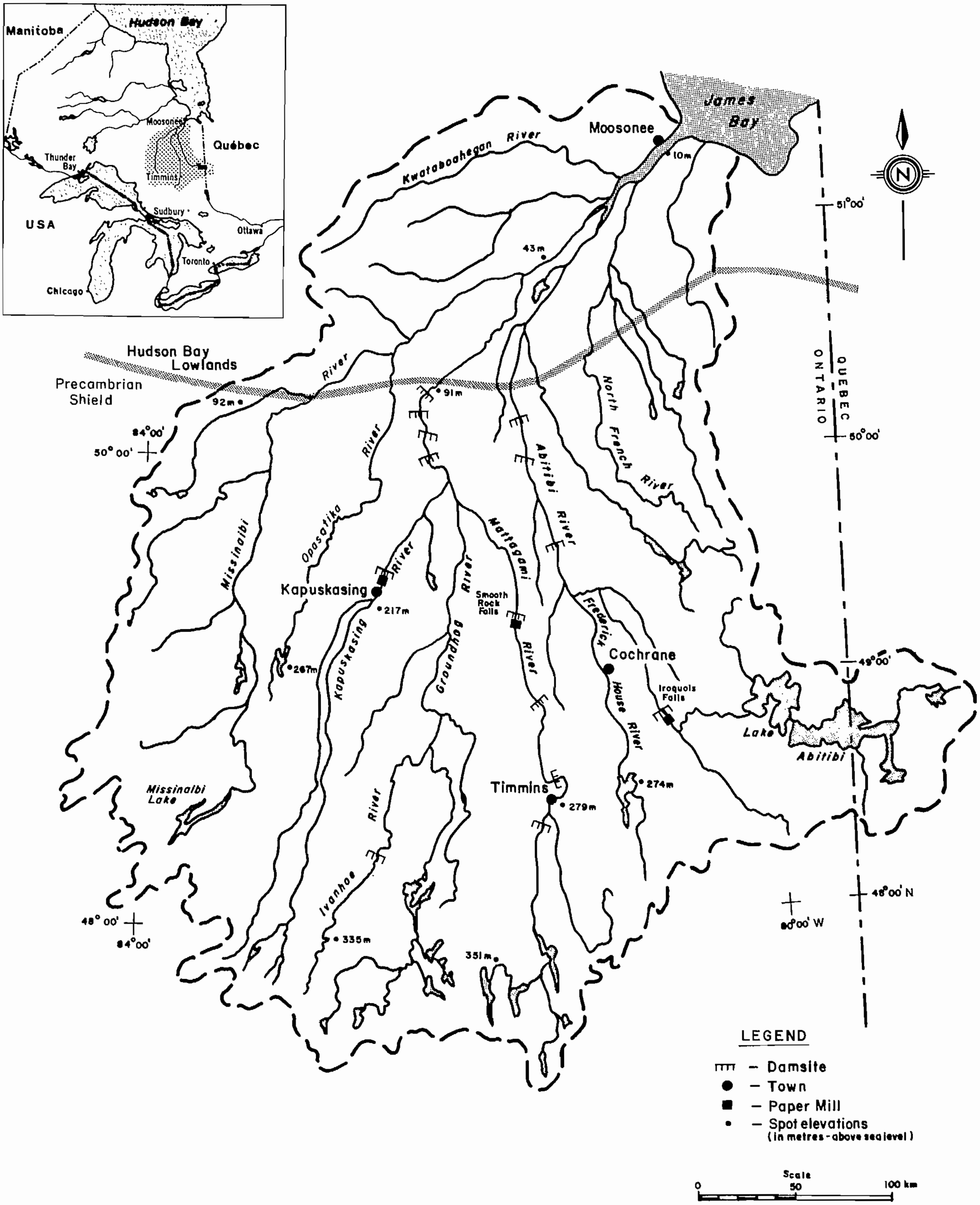

FIG. 1. The Moose River basin, Ontario and its major tributaries.

TABLE 1. Physical characteristics of the Moose River and its major tributaries.

River	Mean flow ($m^3 \cdot s^{-1}$)	Min.	Max.	Stream Order[a]	Length (km)	Drainage basin (km^2)
Moose	780	34	8 270	7	106	109 000
Mattagami	114	0	1 230	6	491	41 672
Kapuskasing	78	0	963	5	324	8 633
Groundhog	145	7	1 810	5	363	12 518
Abitibi	391	20	3 210	5	285	33 987
Frederick House	33	0	436	5	215	4 577
Missinaibi	105	3	1 740	6	430	22 530

[a] As defined by Strahler (1957).

TABLE 2. Climatic conditions at the mouth of the Moose River at Moosonee, Ont.

Temperature (air)	
Annual mean	− 1.1°C
January mean daily maximum	−15.6°C
January mean daily minimum	−26.7°C
July mean daily maximum	22.8°C
July mean daily minimum	10.6°C
Frost free period	86 days
Growing season	154 days
Growing degree days > 5°C	1107
Precipitation	
Annual mean rainfall	66 cm
Annual mean snowfall	241.3 cm

basin is summarized in Table 3, and chemical parameters for the Moose River main channel are given in Table 4. The readings shown are all summer readings when flows were relatively stable; however, flow strongly affects the concentrations of nutrients and trace metals. Spring run-off and snowmelt tends to dilute concentrations; moreover, many parameters can vary considerably throughout the year, but they do not follow a simple seasonal pattern as do major ions which exhibit a strong seasonal trend varying inversely with flow. Daily or short-term variation of major ions are relatively unimportant by comparison (McCrea and Merriman 1981).

The pH readings of the Moose River and its main tributaries range between 6.9 and 8.7, although much of the watershed drains the acidic James Bay peatland. This is probably a reflection of the origin of the headwaters which are located on the Precambrian Shield, but could also be due to the contribution of Devonian clays underlying the peat. The water is moderately soft and buffered, with alkalinity in the 50–70 $mg \cdot L^{-1}$ range. Most of the buffering capacity comes from alkaline bicarbonate ions indicating a fairly stable system. Water colour values are in the 50–100 range (hazen units), typical of most northern Ontario rivers in the Hudson bay drainage area (McCrea et al. 1984). The natural yellow-brown colour of the water reflects high levels of humic acids.

Total dissolved solids (TDS) range from 81 $mg \cdot L^{-1}$ for the Abitibi/Frederick House system to 109 $mg \cdot L^{-1}$ for the Missinaibi system. Elevated turbidity levels in the Frederick House and Abitibi rivers occur because of flooded reservoirs in the clay belt, whereas, the other systems largely originate on the granitic Precambrian Shield. All TDS figures were derived by the formula: TDS = 0.666 × standard conductance (@ 25°C) (Gale and Goodchild 1982).

Benthos

Few studies of benthos have been conducted on the Moose River basin except in several localized investigations. Inventory sampling (Dodge et al. 1987) and studies in conjunction with environmental assessments (EAG 1978) and pollution impact studies (Myslik 1985) have produced a detailed list of species for the watershed.

Both quantitative studies (EAG 1978; Myslik 1985) and qualitative studies (Campbell et al. 1984; McCrea et al. 1984) indicate that a large number of benthic species are present in each river but no one species predominates. As would be expected, species diversity changes according to current, water level fluctuations, turbidity and other factors, and different orders and families can dominate according to the prevailing conditions (McCrea et al. 1984). Diversity is typically low and collections are dominated in numbers by chironomids and tubificids, whereas, biomass is composed mainly of Pleceptera, Odonata, Ephemeroptera and Trichoptera. In polluted areas downstream from pulp and paper mills, severely depressed benthic communities occur for up to 16 km with normal communities absent for up to 64 km downstream of mill effluents (Myslik 1985).

Fish and Fisheries

Distribution

Forty-four species of fishes occur in the Moose River basin (Table 5). Major sport fishes are walleye, lake sturgeon, northern pike and to a lesser extent, lake whitefish and yellow perch. Each are ubiquitous within the basin, but lake whitefish and yellow perch are more common in lakes than rivers.

Because of the short growing season, fish typically have slower growth rates, later ages of maturation and greater longevity than fish of the same species in southern Ontario. Walleye often do not mature until age X, whereas, in southern Ontario they frequently mature at age III. Maximum age can also vary from 10 to 12 yr in the south to 25 yr in the north (Scott and Crossman 1973); however, walleye can exceed age XX in central Ontario (R. A. Ryder, Ministry of Natural Resources, Thunder Bay, Ontario, pers. comm.)

Yellow perch, white sucker and northern pike are the most prevalent species; being found in almost twice as many of the sampled waters as the next most common species

TABLE 3. Chemical analyses of water samples from selected tributaries and the main channel of the Moose River. Values are geometric means (standard deviations in parentheses). Units are mg•L^{-1}, except where otherwise indicated. (OMOE, 1987)

Parameter	Abitibi	Frederick[b] House	Groundhog	Ivanhoe	Kapuskasing	Mattagami	Missinaibi	Moose[c]
Distance from James Bay (km)	283	287	300	459	300	317	324	19
Apparent Colour (Hazen Units)	70	108	65	44[TC]	57	56	—	80
Conductivity @ 25°C (μS•cm^{-1})	121(16)	148	120(41)	125(12)	140(22)	117	163(22)	126
Turbidity (Formazin Units)	40(13)	8.5	3.4(4.7)	4.3(11.0)	2.5(1.2)	4.4(4.3)	1.9(0.2)	—
pH (minimum–maximum)	7.3 (6.9–8.7)	7.8	7.7 (7.1–8.1)	7.8[b]	7.4 (7.1–8.1)	7.3 (6.9–8.7)	8.0[b]	7.2
Total Alkalinity ($CaCO_3$)	48(5)	77	54(9)	60(8)	65(10)	45(8)	62[b]	50
TDS[d]	81	99	80	83	93	78	109	84
Carbon								
— unfiltered total	14.1(1.1)	—	15.1(3.5)	—	15.4(2.4)	14.6(2.3)	—	—
— dissolved organic	15.7(2.9)	—	—	—	—	16.4(4.3)	—	—
Nitrogen — NO_2 + NO_3	0.083(0.061)	—	0.051(0.080)	0.020[b]	0.029(0.035)	0.060(0.120)	0.189	0.167
— Total kjeldahl	0.59(0.24)	0.53	0.49(0.16)	0.410[b]	0.53(0.14)	0.58(0.46)	0.70(0.33)	0.379
Phosphorus								
— filtered reactive orthophosphate	0.026(0.049)	0.013	0.004	0.0016(0.0014)	0.014	0.010(0.064)	0.002	—
— total	0.079(0.102)	0.031	0.020(0.022)	0.021(0.021)	0.022(0.054)	0.039(0.101)	0.011(0.001)	0.0181
Dissolved Oxygen (minimum — maximum)	7.0(2.2) (3.6 - 14.4)	6.6	10.6(2.5) (7.9 - 16.2)	8.7(1.6) (7.0 - 11.0)	6.0(4.2) (0.9 - 14.9)	8.6(3.1) (1.3 - 17.0)	6.0 —	11.0
Number of samples[a]	13 - 77	1	7 - 67	6 - 7	4 - 36	7 - 95	1 - 2	1
Years Collected	1980–86	1983	1980–87	1983	1980–1982	1980–87	1980	1981

[a] Sample sizes vary somewhat depending on analyses. The numbers shown represent the range in the number of samples analysed.
[b] Ministry of Natural Resources, Aquatic Habitat Inventory Surveys (Various locations and times, single samples only).
[c] McCrea et al. (1984).
[d] Calculated from mean conductivity values using formula: TDS = 0.666 × Conductivity 25°C.
[TC] True Colour

TABLE 4. Chemical parameters of the Moose River June 4, 1981 (From McCrea et al. 1984).

Parameter	(mg• L^{-1})
Calcium	19.3
Chloride	1.8
Magnesium	3.8
Potassium	0.54
Silica	2.94
Sodium	1.2
Sulphate	5.7
Aluminum, extractable	0.36
Arsenic, total	0.0005
Copper, total	0.014
Iron, total	0.51
Lead, total	0.004
Nickel, total	0.003
Selenium, total	0.0001
Zinc, total	0.002

(walleye). Most fish sampling was carried out by the Ontario Ministry of Natural Resources aquatic habitat inventory surveys (Dodge et al. 1987). Data were supplemented by localized sampling projects. There is not a great difference in species composition among the major tributaries but some differences occur, perhaps due to variations in turbidity.

The Abitibi/Frederick House tributary, rising on the clay belt, tends to be more turbid than the Mattagami and Missinaibi rivers. The species diversity is slightly higher, with the presence of several species such as freshwater drum, goldeye, mooneye and sauger that are not found, or are extremely rare or localized in the other two watersheds. These are all Pleistocene lake species that have a well developed tapetum lucidum behind the retina which provides a definite ecological advantage in a turbid habitat. The occurrence of goldeye and mooneye in particular likely resulted from the dispersal of fishes across the connection above the Great Lakes of glacial lakes Agassiz and Barlow–Ojibway (Scott and Crossman 1973). Both species are found infrequently elsewhere in the Moose River basin and no where else in northeastern Ontario (Crossman and McAllister 1986). Goldeye prefer the turbid water of large rivers and thrive in the Abitibi system. Freshwater drum is found in the Hudson Bay drainage of both Manitoba and Ontario but reaches the northernmost limit of its range in Ontario at

TABLE 5. Fish species of the Moose River basin (OMNR 1986).

Family and Species	Locations						
	a	b	c	d	e	f	g
Acipenseridae — Sturgeon Family							
Acipenser fulvescens — lake sturgeon	x	x	x	x	x	x	x
Salmonidae — Salmons, Trouts, Whitefishes							
Salmo gairdneri — rainbow trout		*	*	*	*	*	*
Salvelinus fontinalis — brook trout		o	+	+	+	o	+
S. namaycush — lake trout		+	#	#	+	#	+
S. fontinalis × *S. namaycush* — splake					*		
S. fontinalis timagamiensis — aurora trout					■		
Coregonus clupeaformis — lake whitefish	x	x	+	+	x	x	+
C. artedii — cisco (lake herring)		+	+	x	+	#	+
Esocidae — Pike Family							
Esox lucius — northern pike	x	x	x	x	x	x	x
Hiodontidae — Mooneye Family							
Hiodon alosoides — goldeye			x	x	x		
H. tergisus — mooneye		x		x			
Catostomidae — Sucker Family							
Catostomus catostomus — longnose sucker	x	x	x	x	x	x	+
C. commersoni — white sucker	x	x	x	x	x	x	x
Moxostoma sp. — redhorse suckers		x	x	x	#	#	
Cyprinidae — Minnow Family							
Phoxinus eos — northern redbelly dace		#	#	#	#	#	#
P. neogaeus — finescale dace		#	#	#	#	#	#
Couesius plumbeus — lake chub		+	x	+	#	x	#
Notemigonus crysoleucas — golden shiner		#	#	x	x	#	x
Notropis atherinoides — emerald shiner		#	+	x	x	x	x
N. cornutus — common shiner		x	#	#	+	x	x
N. heterolepis — blacknose shiner	x	x	#	x	+	x	#
N. hudsonius — spottail shiner		x	+	x	x	x	x
Pimephales promelas — fathead minnow		#	#	#	x	x	#
Rhinichthys cataractae — longnose dace	x	x	x	x	x	x	x
Semotilus corporalis — fallfish	x	x	#		x		
S. margarita — pearl dace		#	+	#	x	x	
Ictaluridae — Catfish Family							
Ictalurus nebulosus — brown bullhead			#	x			
Gadidae — Cod Family							
Lota lota — burbot		+	x	x	x	x	x
Gasterosteidae — Stickleback Family							
Gasterosteus aculeatus — threespine stickleback	x						
Culaea inconstans — brook stickleback		#	#	+	x	#	#
Pungitius pungitius — ninespine stickleback		+	+	#	#	+	+
Percopsidae — Trout-perch Family							
Percopsis omiscomaycus — trout-perch	x	x	x	+	x	#	x
Centrarchidae — Sunfish Family							
Ambloplites rupestris — rock bass			x	x			
Lepomis gibbosus — pumpkinseed					x		
Micropterus dolomieui — smallmouth bass		*		*	*		*
Percidae — Perch Family							
Perca flavescens — yellow perch	x	x	x	x	x	x	x
Stizostedion canadense — sauger			x	x			
S. vitreum vitreum — walleye	x	x	x	x	x	x	x
Etheostoma exile — Iowa darter		+	#	#	#	x	x
E. nigrum — johnny darter	x	x	x	x	x	x	x
Percina caprodes — logperch	x	x	x	x	x	x	x
Sciaenidae — Drum Family							
Aplodinotus grunniens — freshwater drum		+	x	x			
Cottidae — Sculpin Family							
Cottus bairdi — mottled sculpin	x	x	x	x	x	x	x
C. cognatus — slimy sculpin	x		#		#		#

a — Moose River (main channel)
b — Missinaibi River
c — Abitibi River
d — Frederick House River
e — Mattagami River
f — Groundhog River
g — Kapuskasing River

× — present in river
+ — instream lake
o — in watershed feeder streams
* — introduced
# — inland lake
■ — endangered species (inland lakes)

Lake Abitibi. Sauger, on the other hand, are usually found in more turbid waters usually in association with goldeye, walleye, yellow perch, northern pike and lake whitefish. Sauger are absent in the Moose River proper, possibly due to the limitation imposed by the 15.5°C July isotherm (Ryder et al. 1964) as they do well in turbid waters and have been known to outcompete walleye where conditions of turbidity change in their favour (Scott and Crossman 1973).

The Missinaibi and Mattagami systems have several sites with smallmouth bass. All bass in the system have been introduced (MacKay 1963) and are probably at the limit of their northern range (Shuter et al. 1980). Waters tend to be clearer and warmer in the southern reaches of the basin and smallmouth bass exist in several locations but rarely above 49°N latitude, with the exception of the Missinaibi where there are found at several sites farther north.

Brook trout occur in some tributary feeder streams of the larger rivers, but are rare in main channels.

Contaminants in Fish

The Ontario government monitors fish contaminants from many waters which are angled regularly (OMOE 1986). Mercury, naturally in the bedrock, occasionally exceeds acceptable levels in fish flesh, possibly due to an increase in organic matter following flooding of reservoirs (Jackson 1986). Large old predators will often contain elevated levels due to bioaccumulation. Fish with $0.5\text{–}1.5\ mg\bullet L^{-1}$ of mercury may be eaten by adults (except women of child bearing age) in restricted amounts; however, fish with mercury levels in excess of $1.5\ mg\bullet L^{-1}$ should not be eaten. No restrictions are placed on consumption of fish with less than $0.5\ mg\bullet L^{-1}$ of mercury.

Major Stresses on the Fishery

The development of the Moose River basin has created three anthropogenic stresses detrimentally affecting the fishery: (1) hydroelectric generation, (2) pulp and paper industrial activities; and (3) exploitation by both sport and commercial fisheries.

Hydroelectric Generation

A major impact on fisheries in the Moose River basin has been the development of hydroelectric generation facilities (Table 6). Water level fluctuations between dams, both seasonal and periodic, have caused decreased production and loss of species such as lake sturgeon from some reaches (Payne 1987).

Low water conditions immediately after spawning will affect spawning success as eggs experience variable water temperatures, low oxygen concentrations and exposure to the atmosphere. Fry become trapped in shallow pools and are subjected to heavy mortality through predation, temperature stress and oxygen depletion.

Of the larger fish in the basin, sauger and lake sturgeon are the most vulnerable to hydroelectric effects. Sauger eggs require four weeks to hatch after spawning in mid to late May, and lake sturgeon eggs, although requiring less incubation time, are deposited later than those of sauger.

The mean monthly discharge curve for the Frederick House River over 45 yr is a good example of the wide fluctuations that so drastically affect fish survival (Fig. 2). Generally, there is a slight increase in discharge during the early part of the winter as reservoirs are used to augment low flow for power generation on the Abitibi River. Discharge then drops slightly in April prior to spring freshet. In May, the discharge increases dramatically with spring runoff and then drops rapidly in late May and early June, coinciding with the egg incubation period for many fish species. Discharge continues to drop until late August but then increases again over the autumn.

Due to these wide fluctuations, discharge and profile data have been used to model changing water flow conditions to determine the critical minimum flow for the river. Critical minimum flow is the flow at which the critical reach, that portion of the river which is most sensitive to changes in flow, becomes exposed. Nelson (1980) suggests that if sufficient water flows through the critical reach, adequate amounts of water will be present in less sensitive areas. Adequate flow is that amount of water present at the inflection point of the wetted perimeter — stage discharge relationship. At this point water has covered the stream bed and begins filling the channel according to bank configuration.

Wetted perimeter was calculated using profile and discharge measurements on five reaches surveyed in 1983 (Dodge et al. 1987), using Manning's equation as recommended by Bovee and Milhous (1978). Inflection points occurred at about $10\ m^3\bullet s^{-1}$ (Fig. 3), which may be considered as the critical minimum flow for the river. Even at this flow the actual water depth for these reaches would be less than 0.5 m.

Over the long term, the mean monthly flows for the Frederick House River are above $10\ m^3\bullet s^{-1}$, but there were 4 years between 1939 and 1982 when the mean monthly flow fell to $<1.0\ m^3\bullet s^{-1}$ and 30 years where it dropped to less than $10\ m^3\bullet s^{-1}$ for at least 1 month during the year (Environment Canada 1983) (Fig. 2). In 1977, discharge dropped to $<1.0\ m^3\bullet s^{-1}$ for June, July and August, and in 1982, widely fluctuating discharges resulted in flows going from $5.6\ m^3\bullet s^{-1}$ in April to $32.2\ m^3\bullet s^{-1}$ in May, then decreasing to $1.5\ m^3\bullet s^{-1}$ in June followed by an increase to $26.1\ m^3\bullet s^{-1}$ in July.

TABLE 6. Existing and potential hydraulic sites in the Moose River basin (OMNR 1985b).

Basin	Installed turbine capacity in KW	Power dams no.	Control dams no.	Potential sites	Potential KW
Abitibi	584 864	5	4	69	544 841
Mattagami	491 241	10	14	72	404 017
Missinaibi	0	0	1	35	74 458
North French	0	0	0	1	3 393
Total	1 076 105	15	19	177	1 026 709

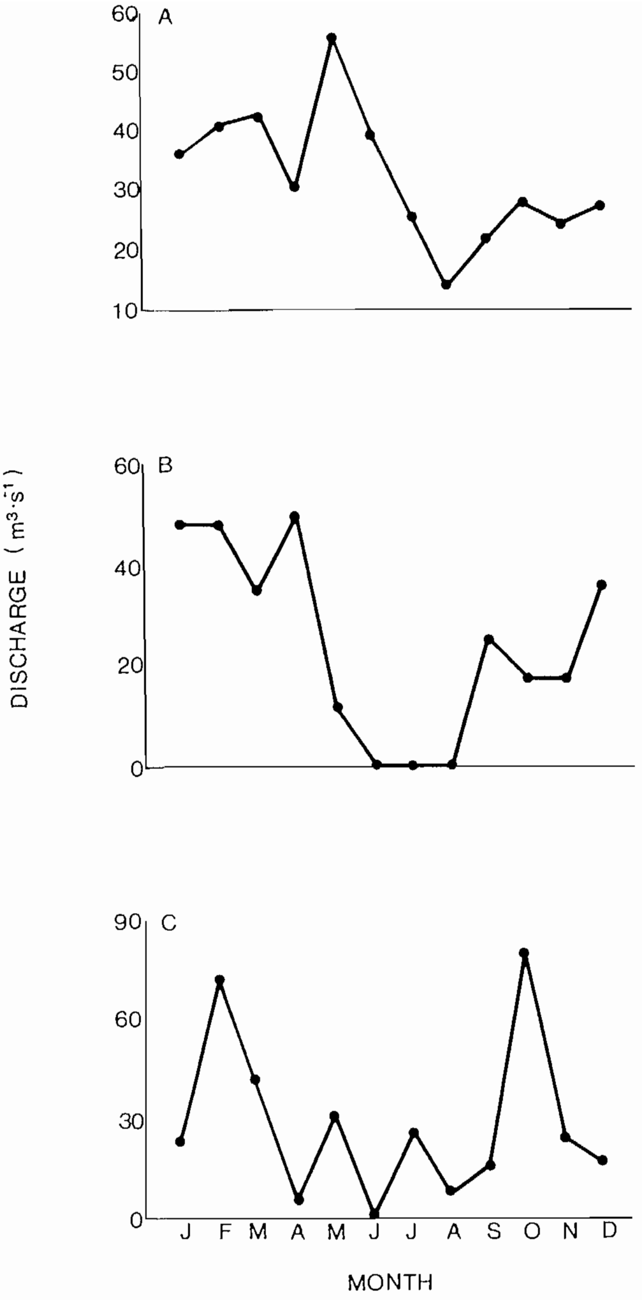

FIG. 2. The mean monthly discharge ($m^3 \cdot s^{-1}$) of the Frederick House River. (A) 45-yr period, (B) 1977, (C) 1982.

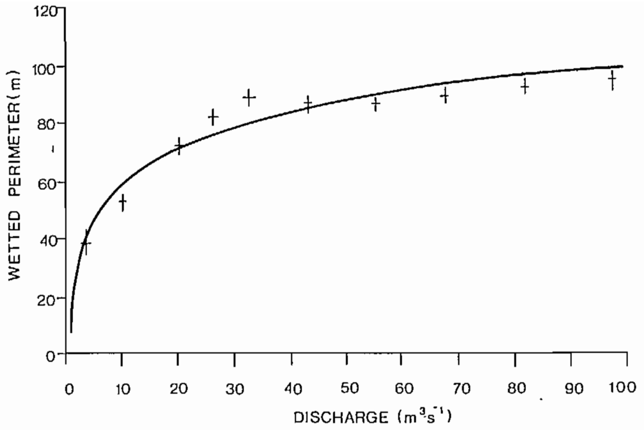

FIG. 3. Hydraulic simulation at Neelands Rapids on the Frederick House River.

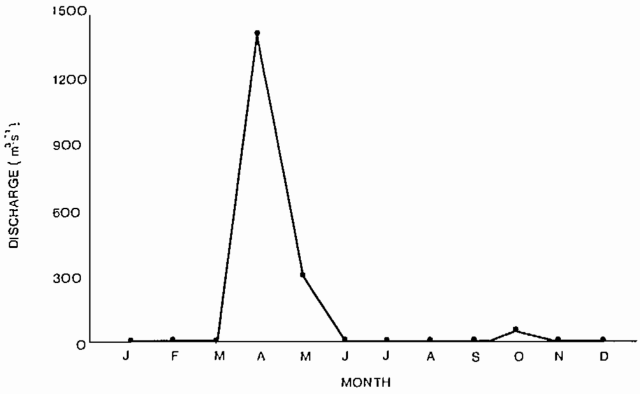

FIG. 4. The mean monthly discharge ($m^3 \bullet s^{-1}$) on Adams Creek.

Another example of the effect of extreme water level fluctuations is at Adams Creek located on the Mattagami River. Adams Creek, once a small, natural stream only a few metres in width, is now used to spill excess water from a storage reservoir circumventing the dams on the Mattagami River (flow above 553.4 $m^3 \bullet s^{-1}$) (Greig et al. 1986). The spill only occurs for about 8 weeks per year, after which the discharge is shut-off completely. The flow rises rapidly from <0.1 $m^3 \bullet s^{-1}$ in late March to about 1 400 $m^3 \bullet s^{-1}$ in late May. There are occasional flows in the fall in years of high water (Fig. 4).

This rapid flush of Adams Creek has carved a new channel from the reservoir to the creek and greatly enlarged the actual creek bed creating a large sediment load which is deposited into the Mattagami River. Water in the creek becomes very turbid with secchi disc readings of only a few centimetres. Severe erosion occurs along the entire length of the stream; clay cliffs between 20 and 40 m in height now form banks of the channel which is up to 100 m wide.

Fish such as lake sturgeon enter Adams Creek either from the Mattagami River when spawning or are washed over the spillway during high flow periods. When the discharge is halted these fish are often stranded in pools, and migration or escape becomes impossible. Mortality occurs when pools become anoxic or freeze-out.

Another deleterious factor affecting fish is winter drawdown of some lakes in the system for low flow augmentation of power production. The water elevation in Mesomikenda Lake on the headwaters of the Mattagami River (Fig. 5) is drawn down about 3 m beginning in early January, and does not begin to rise again until early May during spring run-off. Mesomikenda Lake originally contained native lake trout. After construction of a control dam in 1916, water levels in the lake were raised and lake trout spawning areas became heavily silted. Over the years, lack of recruitment has extirpated the lake trout population in the lake. Similarly, in Lake Abitibi (Fig. 5) with a mean depth of only 3.5 m, extreme lake drawdown in the winter of up to 2.7 m has been responsible for the population decline of fall spawning species such as lake whitefish.

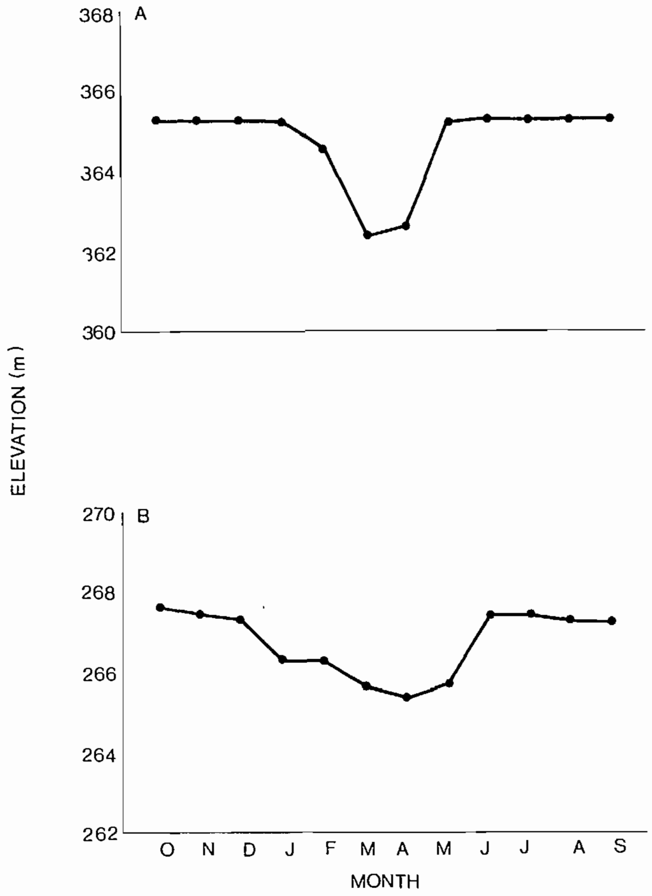

FIG. 5. Water level elevations (m) by month. (A) Beaver Lake, (B) Lake Abitibi.

Measures designed to protect fish habitat are needed. Hydraulic simulations to determine minimum required flows should be done on critical reaches of tributaries in the basin. Minimum flow requirements need to be established in sensitive areas. Spawning and incubation periods for fish species such as walleye, sauger and lake sturgeon, should be considered in areas with manipulated flow regimes to prevent high mortalities of eggs and fry following spring run-off. Likewise, winter drawdown of major reservoirs should be timed to prevent disruption of fall spawners and still provide enough available habitat under the ice. The development of new sites should avoid critical spawning areas or should incorporate measures to reduce the impact on the fishery. For example, on Mesomikenda Lake, mid-winter drawdown is delayed by a few weeks in an attempt to allow the eggs to hatch prior to freeze-out (Kindree and Brousseau 1984). Needs of both the power industry and fishery should be used to determine water management schemes in sensitive areas.

Pulp and Paper Industry

The actual harvesting of lumber to supply three major pulp and paper mills in the basin has likely had a minimal impact on fish habitat. Controlled cut prescriptions usually provide adequate buffer strips to prevent shoreline erosion; however, forest road crossings can destroy fish habitat. Road crossings should avoid spawning areas, allow for unobstructed migrations of fish, maintain water quality and be constructed at times to avoid spawning and incubation periods.

Log driving and mill effluents, however, have severely degraded fish habitat in the vicinity of the mills. For example, the Kapuskasing River has been used for log drives since the 1920's. Over 500 000 m^3 of 1.3 m length logs are floated down the river annually. Logs are slashed and piled parallel to the river so the rising water in the spring floats a portion of the wood into the current. The remainder is bulldozed into the river along with large quantities of soil causing siltation downstream of the landing. Logs float freely downstream to a major holding facility about 21 km above the mill at Kapuskasing. Immediately above the mill, approximately 5–7 km of the river is completely covered and blocked with logs (OMOE 1976).

In areas of fast water there is little effect on benthic communities, but in bark and fibre depositional areas, reduction in invertebrate taxa and fouling of the streambed occurs (Bowman 1984). The buildup of bark and wood fibre may also result in the reduction in recruitment of fishes and survival of eggs and fry (Kramer and Smith 1966). Low dissolved oxygen levels (less than 2.0 $mg \bullet L^{-1}$) can occur upstream of the mill, principally in the 18 km reach used for log storage. This has a significant effect on the downstream assimilative capacity of the river and allowable loadings from the mill (Bowman 1984). Alternatives to log driving should be considered, and log landings should be designed to reduce the input of debris when logs are pushed into the river.

The downstream effects of mill effluent include a build-up of organic debris, adverse changes in water chemistry, particularly dissolved oxygen, and disruption of benthic communities. Decomposing organic wastes (eg. waste liquors) and fibrous material (eg., bark fines, slivers, and fibers) exert a high demand for dissolved oxygen (OMOE 1977). Oxygen depletion and the covering of the river bottom with these wastes destroy fish spawning areas and interfere with production of fish food organisms. Smith et al. (1966) showed that sulphate and groundwood wastes decrease the hatchability of fish eggs and survival of fish fry as well as affecting a number of sublethal physiological changes in mature fish. Oxidation of wastes at the sludge-water interface may reduce dissolved oxygen to critical concentrations, as well as releasing toxic levels of by-products such as hydrogen sulphide (Colby and Smith 1967). Stein and Denison (1966) found that sludge deposits from a sulphite pulp mill can utilize 3.6 g $O_2 \bullet d^{-1} \bullet m^{-1}$.

On the Abitibi River there are large accumulations of solids directly below the mill at Iroquois Falls and extensive fibrous deposits for a distance of about 80 km downstream. On the Mattagami River deposits of bark debris, bark mats and areas of gas release are evident. Foam occurred up to 5 km downstream of the mill at Smooth Rock Falls. The most pronounced accumulation of bark debris occurred from 30 to 43 km downstream. There may be quiescent zones downstream of this point where oxidation of settled solids could cause elevated oxygen demand. On the Kapuskasing and Abitibi rivers, areas where organic sediment demands are most predominant usually occur more than 40–55 km below the pulp mills (OMOE 1977).

An example of high dissolved oxygen demand can be shown for the Abitibi River. During a September 1967 survey (OWRC 1968) when discharge was 229 $m^3{\bullet}s^{-1}$, dissolved oxygen levels averaged close to 7.0 $mg{\bullet}L^{-1}$ but twice fell below 4.0 $mg{\bullet}L^{-1}$. On occasion, however, when the paper mill is not in operation, the flow in the river below the mill is reduced to $<0.1\ m^3{\bullet}s^{-1}$. Without flow, the river stagnates, reducing its natural ability for reoxygenation, and allows suspended materials to settle onto river beds. During summer periods of low flows and elevated temperatures, deoxygenation wastes from the mill probably reduce the dissolved oxygen in the river to $<2.0\ mg{\bullet}L^{-1}$ (OWRC 1968).

Similarly, on the Mattagami River, dissolved oxygen was significantly depressed adjacent to and downstream from the mill. Dissolved oxygen levels dropped from 7.8 $mg{\bullet}L^{-1}$ above the mill to 4.3 $mg{\bullet}L^{-1}$ (47 % saturation) below the mill, and recovered only partially (6.5 $mg{\bullet}L^{-1}$) 43 km further downstream (Fig. 6). In 1981, a dissolved oxygen depression of $<3.5\ mg{\bullet}L^{-1}$ was observed on the Mattagami River (OMOE 1983). The effluent pH averaged 5.4, reducing the ambient pH from 7.7 to ph 7.4–7.5. BOD increased from an ambient condition of 1.4 $mg{\bullet}L^{-1}$ adjacent to the mill outfall. Sodium concentrations increased tenfold downstream of the mill while conductivity measurements indicated a significant increase of dissolved solids (OMOE 1977).

The distribution and abundance of benthic organisms in the Abitibi River indicated that the river was heavily polluted for a distance of 60 km below the mill site at Iroquois Falls, and recovery was incomplete even at 80 km downstream (German 1968). On the Mattagami River bottom fauna communities have been virtually eliminated adjacent to the mill effluent discharge and severe depression of aquatic invertebrate populations (based on comparisons at locations upstream of the discharge point) exist at least 16 km downstream of the mill at Smooth Rock Falls (OMOE 1977).

The data clearly indicate that flows below the pulp and paper mills should be maintained during critical periods to prevent deoxygenation of downstream waters, and waste treatment and other measures such as settling ponds, should be used to decrease the bulk of the discharge.

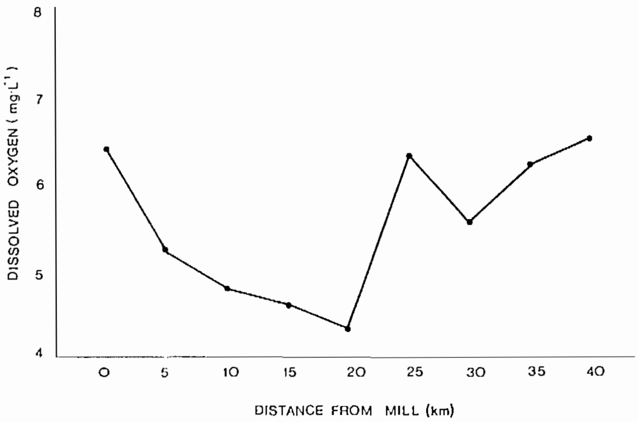

FIG. 6. Dissolved oxygen concentration ($mg{\bullet}L^{-1}$) downstream from the pulp and paper mill on the Mattagami River (from OMOE 1977).

Exploitation

Before 1900, fish harvest from rivers was restricted to nomadic bands of Indians and fur traders. Both sport and commercial exploitation increased with the influx of settlers following the development of the mining and pulp and paper industries. Very few fish stocks would have been seriously stressed because the human population remained low and the distance to markets precluded the development of any major commercial fisheries. Despite government attempts to encourage settlement in the area, the basin has remained sparsely populated with only about 100 000 people, approximately 0.9 $persons{\bullet}km^{-2}$.

Catches of walleye, lake whitefish, northern pike and lake sturgeon sustained minor commercial fisheries on the Mattagami, Abitibi, Groundhog and Moose rivers. The lake sturgeon fishery on the Mattagami river has operated since 1917. Between 1927 and 1963 annual harvests have fluctuated widely from 0.06 to 1.63 $kg{\bullet}ha^{-1}$ with an average of 0.64 $kg{\bullet}ha^{-1}$. On the Abitibi River the mean annual harvest since 1935 was 0.21 $kg{\bullet}ha^{-1}$, while on the Moose River the lake sturgeon commercial fishery harvests about 400 kg annually. Today, there are only a few commercial fisheries in the basin licensed to take lake whitefish and lake sturgeon. Harvest of both species is controlled by small quotas in addition to maximum length limits on sturgeon.

Sport fishing in the rivers of the Moose River basin is seasonal with the majority of the angling pressure occurring near the spawning areas (usually associated with rapids and chutes) following spawning. Fishing pressure drops by mid July when fish become dispersed and more difficult to catch.

For instance, on a 30 km stretch of the Mattagami River in 1983, about 8 000 angler hours were spent. Over 98 % of the fishing pressure occurred in the vicinity of spawning areas and over 70 % of the pressure occurred in the 6-wk period following spawning (May 21–July 1). Of the 1 660 fish kept, northern pike comprised 62.3 %, walleye 33.5 % and yellow perch 3.5 %. The catch per unit effort for all fish caught was 0.22 $fish{\bullet}h^{-1}$. On a 45 km stretch of the Groundhog River in 1984, over 12 000 angler hours were spent. Anglers harvested about 4 600 kg of lake sturgeon, 300 kg of northern pike and 25 kg of walleye. Over half of the lake sturgeon harvest came from a small area on the river known as ''The Pot'' where an estimated 175 $kg{\bullet}ha^{-1}$ of sturgeon were taken. This level of angling intensity constitutes considerable overfishing (Nowak and Jessop 1987). In contrast, an aerial survey of boats of the entire Moose River main channel in 1985 indicated only about 10 anglers per day on weekends.

There are probably less than 100 000 angler $days{\bullet}yr^{-1}$ on all rivers in the Moose River basin. Overall, fishing is light, with only a few local overharvest problems and some depletion of stocks evident as a result of sport fishing.

Although fishing pressure is low in the basin, low productivity tends to make the fisheries vulnerable to even low levels of exploitation. Harvests are concentrated on only a few species in specific locales. The slow growing, late maturing nature of several species, particularly lake sturgeon, make the protection of brood stock extremely important in both sport and commercial fish management. This can be achieved by imposing fishing regulations such as maximum size limits and slot limits (Brousseau and Armstrong 1987) in which the majority of breeding fish are protected and harvest of large and trophy fish is reduced.

Most important fish species in the Moose River basin are managed by creel limits and closed seasons during the spawning period. Experimental angling regulations for three lakes in the Abitibi watershed include slot limits of 43–60 cm for walleye to protect the brood stock (Brousseau and Armstrong 1987). A maximum size limit on northern pike of 70 cm with a limit of 1 pike above this size per angler per day is soon to be implemented on another lake in the basin. Trophy fish regulations for brook trout in northern rivers, which limit the number of trout over 40 cm to one per angler per day and maximum size limits on lake sturgeon taken commercially in the Moose River (Threader and Brousseau 1986) and on other rivers in the basin are also being implemented. Additional measures required are more sanctuaries in vulnerable locations to protect spawning fish (Nowak and Jessop 1987), the control of access in sensitive areas, and encouragement to anglers to harvest underutilized species such as goldeye, yellow perch and lake whitefish.

All these techniques should be applied on a more intensive basis on each river in the basin where overexploitation is a problem. In other areas where exploitation is not a major stress, access could be encouraged to distribute the angling pressure over a larger area.

Fish Yields

Fish productivity studies of lotic systems in Ontario have usually been done on moderately small, coldwater trout streams.

About 25 % of all sport fishing in the Moose River basin occurs on rivers, even though 23 000 lakes are contained within the basin of which 40 lakes are greater than 1 000 ha. There is an increasing demand for both sport and commercial fishing but very little is known about the capacity of these rivers to produce fish. In the past 6 yr, studies have been done on standing stocks of fish in the Frederick House River and on lake sturgeon in the Moose River and four of its tributaries, to gain a better understanding of potential yields of fish to manage rivers more effectively.

The morphoedaphic index (Ryder 1965) is widely used in Ontario for estimating fish yield in lakes, but no indicator of potential has been developed to the same degree for Ontario river fisheries (MacRitchie 1981). Estimators of fish catch have evolved from studies of African flood plain rivers (Welcomme 1976), the Danube River (Kölbing 1978; Holčík and Bastl 1977) and the Amazon River (Bayley 1981). Simple morphological and biological parameters appear to provide an excellent basis for fish-catch predictions in these rivers. Similar catch data, however, do not exist for large rivers in Ontario. Potential harvest or yield estimates can be obtained for individual species (see Beverton and Holt 1957; Ricker 1975), but these methods require an extensive knowledge of growth, mortality, fecundity rates, year-class structure and other demographic characteristics of fish populations.

Standing-stock estimates were considered the best basis for assessing fisheries in the Moose River basin. These estimates would eventually provide the data base needed to test the various abiotic and biotic parameters for correlation to fisheries potential. The only practical way to obtain standing stock estimates was to undertake mark and recapture studies.

These techniques were applied to a 14 km reach of the Frederick House River in the spring of 1981 and 1983. Fish were captured using 1.2, 1.8, and 2.4 m trap and hoop nets. Walleye, sauger, northern pike and lake sturgeon were tagged with either a metal jaw tag or plastic streamer tag attached anterially to the dorsal fin. Other fish were marked with a combination of fin clips which was unique for a capture site and valid for a three day period. The modified Schnabel method (Ricker 1975) provided the narrowest confidence limits for all species except lake sturgeon, which was suitable only to an adjusted Peterson estimate (MacRitchie 1983).

The total number of fish estimated for the 14 km reach of the Frederick House River was 6 232 (Table 7). Goldeye was the most abundant species (20.4 fish•ha^{-1} followed by three sucker species. Sauger, walleye, lake sturgeon and northern pike existed at much lower densities (<3.3 fish•ha^{-1}). Other fishes, caught in numbers which precluded population estimates were mooneye, lake whitefish, burbot, yellow perch, lake herring, brown bullhead, and rock bass.

The total standing stock was estimated at 4 669.5 kg or 47.6 kg•ha^{-1}. Lake sturgeon comprised 37 % of the biomass of the standing stock followed by goldeye (17.0 %) and longnose sucker (16.0 %). The standing stock estimate is similar to the Bobrza River in Poland and the Needle Branch River in the United States (Welcomme 1985). The total yield was 1 117.2 kg or 11.4 kg•ha^{-1}•yr^{-1} and the production/biomass ratio was 0.24. This estimate is less than estimates for temperate and tropical rivers listed by Welcomme (1985) but higher than those on eastern James Bay in Northern Quebec (Roy 1989). Standing stock estimates are conservative, however, since they include only fish vulnerable to the gear and it is not possible to compare them directly with those by Welcomme (1985). Low productivity in the Frederick House River may also be attributed to the short growing season, low fertility of the water, the high level of inorganic turbidity and environmental perturbations caused by a hydroelectric dam upstream.

From 1980 to 1985, studies on lake sturgeon standing stocks were done on the Moose, Frederick House, Abitibi, Mattagami and Groundhog rivers. Gill nets (mesh sizes of 3.8–30.5 cm) were used to capture sturgeon, along with some trap nets and baited hooks. Length, weight, and sex were recorded when fish were tagged with streamer tags or metal jaw tags inserted through muscle anterior to the dorsal fin. Adjusted Peterson and Schnabel methods were used for population estimates (Ricker 1975).

Standing stock estimates for the Frederick House, Abitibi, Groundhog and two sites on the Mattagami River are in Table 8. The Moose River was not included because of problems defining the steady reach. Estimates for numbers of fish ranged from 0.17 to 7.2 fish•ha^{-1} with corresponding standing stocks of 1.0–84.7 kg•ha^{-1}. Lake sturgeon populations in the Frederick House, Abitibi and Groundhog rivers appear to be healthy, whereas, the Mattagami River population exists in low numbers. Commercial over-harvest and water level fluctuations during spawning may have caused the decline in the Mattagami River population (Payne 1987).

TABLE 7. Fish standing stock and yield estimates at Neeland's Rapids in the Frederick House River, 1981 and 1983 combined, from MacRitchie (1983).

Species	Number of fish	Yield ($kg \cdot yr^{-1}$)	Standing stocks (kg)	P/B
goldeye	2 000	121.5	800.0	0.15
longnose sucker	1 531	49.4	745.7	0.07
redhorse sucker	1 077	85.4	581.5	0.15
white sucker	865	156.9	516.8	0.30
sauger	328	15.5	89.0	0.17
walleye	196	34.4	84.3	0.41
lake sturgeon	155	625.3	1 751.1	0.36
northern pike	80	28.8	101.1	0.28
Totals	6 232	1 117.2	4 669.5	
Mean				0.24

The low P/B ratio illustrates the sensitivity of lake sturgeon to overexploitation. Long-term yields of only 0.2 $kg \cdot ha^{-1} \cdot yr^{-1}$ might be expected from healthy populations in good habitat. Threader and Brousseau (1986) suggest that lake sturgeon in the Moose River can only withstand an exploitation rate of 1.8 % of the population per annum. This low harvest, which is lower than for any other species in Ontario, is necessary because of the sturgeon's slow growth, late maturation (15–25 yr) and intermittent spawning (Brousseau 1987).

Fish movement throughout the river systems appeared minimal. The majority of recaptures were within a few kilometres of the original tagging site. Ninety-four percent of fish recaptured on the Frederick House River were found within 5 km of the tagging site and 80 % of the sturgeon recaptured on the Moose River were taken within 1 km of the tagging site. All recaptures had moved less than 5 km during the 3 year period. Small numbers of sturgeon migrate several kilometres, usually associated with pre and post spawning migrations, although there appears to be a large, primarily sedentary population and a smaller roving component. This behaviour is another factor indicating the vulnerability of the stock to rapid overharvest if left unprotected.

Future Needs

Protection of fish habitat and conservation of brood stocks are two fundamental actions that must be considered for management of fisheries in rivers of the Moose River basin. Moreover, the inherently low production of fish, induced by harsh climatic conditions and resultant short growing seasons coupled with culturally induced perturbations, must be considered when measures are taken to protect vulnerable fish stocks.

Fisheries management in the Moose River basin is hampered by a lack of knowledge of the basic physical, chemical and biological properties of large rivers. Aquatic habitat inventory surveys are needed for the Abitibi, Missinaibi and Moose rivers to complement existing surveys on other large rivers in the basin. Hydraulic simulation modelling is required on controlled rivers to determine minimum flow requirements in critical reaches and the effects of water level fluctuations. In addition, hydroelectric drawdown needs to be quantified to determine effects on fish habitat and production. Standing stock of fish and sustainable yield estimates are also vital for future management of the fisheries resource of the Moose River basin.

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TABLE 8. Standing stock and yield estimates of lake sturgeon from selected reaches in the Frederick House, Abitibi, Mattagami, and Groundhog rivers (from Nowak and Jessop 1987; Payne 1987).

River	Reach area (ha)	Number of fish	Standing stocks ($kg \cdot ha^{-1}$)	Yield ($kg \cdot ha^{-1} \cdot yr^{-1}$)	P/B
Frederick House	98	155	17.8	0.79	0.35
Abitibi	1002	944	7.1	0.26	0.03
Mattagami (1)	396	114	2.0	0.27	0.13
Mattagami (2)	189	33	1.0	0.16	0.17
Groundhog	1168	8429	84.7	3.90	0.04

References

Bayley, P. B. 1981. Fish yield from the Amazon in Brazil. Comparison with African river yields and management possibilities. Trans. Am. Fish. Soc. 110: 351–359.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. U. K. Min., Agric. Fish., Fish. Invest. (Ser. 2) 19: 533 p.

Bovee, K. D., and R. Milhous. 1978. Hydraulic simulation in instream flow studies: theory and techniques. Co. Inst. Flow Ser. Gr. West. Energy and Land Use Team. Fish and Wildlife service. U.S.D.I. 131 p.

Bowman, A. B. 1984. Biological survey of the Kapuskasing River. Ont. Min. of the Environ. Water Resources Assessment Unit, Sudbury, Ont. 55 p.

Brousseau, C. S. 1987. The lake sturgeon (*Acipenser fulvescens*) in Ontario. *In* C. H. Olver [ed.] Proceeding of a workshop on the lake sturgeon (*Acipenser fulvescens*). Ont. Fish. Tech. Rep. Ser. No. 23: 99 p.

Brousseau, C. S. and T. A. Armstrong. 1987. The role of size limits in walleye management. Fisheries, Vol. 12, No. 1: 2–5.

Campbell D. E., R. E. Kwiatkowski, and R. C. McCrea. 1984. A study of benthic communities in five rivers of the Hudson Bay Lowland, Canada, Environment Canada, Inland Waters Directorate, Water Quality Branch, Burlington, Ont.

Colby, P. J., and L. L. Smith. 1967. Survival of walleye eggs and fry on paper sludge deposits in the Rainy River, Minnesota. Trans. Am. Fish. Soc. 96(3): 278–296.

Crossman, E. J., and D. E. McAllister. 1986. Zoogeography of freshwater fish of the Hudson Bay drainage, Ungava Bay and the Arctic Archipelago, p. 53–104. *In* C. H. Hocutt and E. O. Wiley [ed.] The zoogeography of North American freshwater fish. John Wiley & Sons, NY.

Dodge, D. P., G. A. Goodchild, I. MacRitchie, J. C. Tilt, and D. G. Waldriff. 1987. Manual of instructions: aquatic habitat inventory surveys. Ont. Min. of Nat. Res., Toronto, Ont. 246 p.

Environment Canada. 1983. Historical streamflow summary, Ontario, to 1982. Inland Waters directorate, Ottawa, Canada. 523 p.

Environmental Applications Group Limited. 1978. Environmental baseline studies for Onakawana project. Report for Onakawana Development Limited, Ontario Hydro, Toronto, Ont.

Gale, G. E., and G. A. Goodchild. 1982. Review and reformulation of the relationship between standard conductance and total dissolved solids. Ont. Min. of Nat. Res., Toronto, Ont. 82 p.

German, M. J. 1968. Biological survey of the Abitibi River. Ont. Min. of the Env. Library, Toronto, Ont. 24 p.

Greig, L. A., L. P. Rattie, R. R. Everitt, and M. L. Jones. 1986. Potential environmental effects of the proposed Mattagami hydroelectric extension project. ESSA Environmental and Social Systems Analysts Ltd., Toronto, Ont. 60 p.

Holčík, J., and I. Bastl. 1977. Predicting fish yield in the Czechoslovakian section of the Danube River based on hydrological regime. Int. Rev. Gestamen Hydrobiol. 62(4): 523–532.

Jackson, T. A. 1986. Methyl mercury levels in a polluted prairie river-lake system: seasonal and site-specific variations, and the dominant influence of trophic conditions. Can. J. Fish. Aquat. Sci. 43: 1873–1887.

Kindree, M., and C. S. Brousseau. 1984. MNR — Hydro team up on lake trout project. Landmarks (3): 30.

Kölbing, A. 1978. The European method of fish harvest prediction in fluvial systems. Environ. Biol. Fish. 3(3): 249–251.

Kramer, R. H., and L. L. Smith. 1966. Survival of walleye eggs in wood fibre. Progr. Fish. Cult. 28(2): 79–82.

MacKay, H. H. 1963. Fishes of Ontario. Ont. Dep. Lands and Forest, Toronto, Ont. 292 p.

MacRitchie, I. 1981. Towards a river fishery potential model. Ont. Min. of Nat. Res., Cochrane, Ont. 22 p.

1983. Fish production at Neelands Rapids in the Frederick House River. Ont. Min. of Nat. Res., Cochrane, Ont. 9 p.

McCrea, R. C., and J. C. Merriman. 1981. Water quality in the Moose River — a pilot study, 1977–1978. Report Series No. 70, Inland Waters Directorate, Ottawa, 9 p.

McCrea, R. C., R. E. Kwiatkowski, D. E. Campbell, P. P. McCarthy, and T. A. Norris. 1974. An investigation of contaminants and benthic communities in the major rivers of the Hudson Bay Lowland, Ontario. Canada Inland Water Directorate, Ontario Region, Burlington, Technical Bulletin No. 131: 63 p.

Myslik, G. 1985. 1981 and 1985 biological surveys of the lower Kapuskasing River, Kapuskasing, Ontario. Technical memorandum, Ontario Min. of the Environ. Sudbury, Ontario. 12 p.

Nelson, F. A. 1980. Evaluation of four instream flow methods applied to four trout rivers in southwest Montana. U. S. Dept. of the Interior, Fish and Wildlife service. 105 p.

Nowak, A. M., and C. S. Jessop. 1987. Biology and management of the lake sturgeon in the Groundhog and Mattagami Rivers, Ontario. *In* C. H. Olver [ed.] Proceedings of a workshop on the lake sturgeon (*Acipenser fulvescens*). Ont. Fish. Tech. Rep. Ser. No. 23: 20–32.

Ontario Ministry of Natural Resources. 1983. Cochrane district land use guidelines. Ont. Min. of Nat. Res., Cochrane, Ont. 84 p.

1985a. Moosonee district background information. Ont. Min. of Nat. Res., Moosonee, Ont. 167 p.

1985b. Ontario's water power sites. Pub. No. 3460, Toronto, Ont. 69 p.

1986. Ontario fish species distribution system. Ont. Min. of Nat. Res. Fisheries Branch, Toronto, Ont.

Ontario Ministry of the Environment. 1976. Operation of a pulp and paper mill, its uses of and effects upon the Kapuskasing River. Ont. Min. of the Environ., Industrial Abatement Section, Timmins, Ont. 83 p.

1977. The Mattagami River, a preliminary water quality assessment. Ont. Min. of the Environ., Industrial Abatement Section, Timmins, Ont. 80 p.

1983. Report of the assimilative capacity of the Mattagami River downstream from Smooth Rock Falls. Ont. Min. of the Environ., Technical Support Section, Sudbury, Ont. 39 p.

1986. Guide to eating Ontario sport fish. Ont. Min. of the Environ., Toronto, Ont. 281 p.

1987. Water quality data, Ontario lakes and streams, 1980–1987. Ont. Min. of the Environ., N.E. Region, Water Resources Branch.

Ontario Water Resources Commission. 1968. The Abitibi River below Iroquois Falls, a water use study. Ont. Min. of the Environ. Library, Toronto, Ont. 24 p.

Payne, D.A. 1987. Biology and population dynamics of lake sturgeon (*Acipenser fulvescens*) from the Frederick House, Abitibi and Mattagami Rivers, Ontario. *In* C. H. Olver [ed.] Proceedings of a workshop on the lake sutrgeon (*Acipenser fulvescens*). Ont. Fish. Tech. Rep. Ser. No. 23: 10–19.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

Roy, D. 1989. Physical and biological factors affecting the distribution and abundance of fishes in rivers flowing into James Bay and Hudson Bay, p. 159–171. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Ryder, R. A. 1965. A method of estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. 94: 214-218.

RYDER R. A., W. B. SCOTT, AND E. J. CROSSMAN. 1964. Fishes of northern Ontario, north of the Albany River. Roy. Ont. Mus., University of Toronto Life Sci. Div. Contrib. 60: 30 p.

RYDER, R. A., AND J. PESENDORFER. 1989. Large rivers are more than flowing lakes: a comparative review, p. 65–85. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can., 184: 966 p.

SHUTER, B.J., J. A. MACLEAN, F. E. J. FRY, AND H. A. REGIER. 1980. Stochastic stimulation of temperature effects on first-year survival of smallmouth bass. Trans. Am. fish. Soc. 109: 1–34.

SMITH, L. L., R. H. KRAMER, AND D. M. OSEID. 1966. Long term effects of conifer-groundwood paper fibre on walleyes. trans. Am. Fish. Soc. 95: 60–70.

STANFIELD, R., J. RILEY, B. MACKAY, AND R. C. BURDETT. 1972. Biological studies of the Onakawana Area. Task Force Onakawana Working Paper #3. Ont. Min. of Nat. Res., Wildlife Research, Toronto, Ont. 60 p.

STEIN, J. E., AND J. G. DENISON. 1966. *In situ* benthal oxygen demand of cellulosic fibers. Adv. Water Pollut. Res. 3: 181–193.

STRAHLER, A. N. 1957. Quantitive analysis of watershed geomorphology. Trans. Am. Geophys. Union 38: 913-920.

THREADER, R. W., AND C. S. BROUSSEAU. 1986. Biology and management of the lake sturgeon in the Moose River, Ontario. N. Am. J. Fish. Man. 6: 383-390.

WELCOMME, R. L. 1976. Some general and theoretical considerations on the fish yield of African rivers. J. Fish. Biol. 8: 351-364.

1985. River Fisheries. FAO Fisheries Technical Paper 262, Rome. 330 p.

Physical and Biological Factors Affecting the Distribution and Abundance of Fishes in Rivers Flowing into James Bay and Hudson Bay

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Abstract

ROY, D. 1989. Physical and biological factors affecting the distribution and abundance of fishes in rivers flowing into James Bay and Hudson Bay, p. 159–171. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The rivers of northern Québec flow into James Bay, Hudson Bay and Ungava Bay. Except for sport fishing southwest of this area for which few data are available, subsistence fishing by natives is the only major use of the aquatic resources. North of the boreal forest, fishing occurs mainly near the coast, in the estuaries and downstream sections of rivers. After modest efforts, commercial fishing declined and now takes only small quantities of Atlantic salmon and Arctic char. Large rivers in this region are generally not good permanent habitats for fish. Fish prosper only near the few large lakes and estuaries which they use as temperature refugia during winter; moreover, there are often substantially fewer fish in rivers than in adjacent lakes. Severe weather conditions, rapid fluctuations in water levels, fast currents, low productivity and accumulations of ice and frazil restrict the year-long maintenance of abundant and diversified fish communities. Fish species found under these conditions must be highly adaptive and have the ability to survive despite low levels of food resources. Estuaries, downstream sections of rivers, and lakes often serve as a refugia from winter stresses in both marine and lotic environments. Factors that most limit fish catches from northern Québec are low levels of abundance and the high mercury content in fish, in natural environments but specially in the new reservoirs and their outfalls.

Résumé

ROY, D. 1989. Physical and biological factors affecting the distribution and abundance of fishes in rivers flowing into James Bay and Hudson Bay, p. 159–171. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Les rivières septentrionales du Québec s'écoulent dans la baie James, la baie d'Hudson et la baie d'Ungava. À l'exception de la pêche sportive dans la partie sud-ouest de cette région, qui a été peu étudiée, la pêche pour la subsistance par les autochtones constitue la seule utilisation importante des ressources aquatiques. Au nord de la forêt boréale, la pêche se fait surtout le long de la côte, dans les estuaires et dans les tronçons aval des rivières. Après quelques modestes tentatives, la pêche commerciale a subi un déclin et n'est responsable que d'une petite partie des captures du saumon atlantique et de l'omble arctique. Les grandes rivières de cette région ne constituent généralement pas de bons habitats permanents pour les poissons. Les populations ne prospèrent que près des quelques grands lacs et estuaires qui leur servent de refuge durant le froid de l'hiver; en outre, il y a souvent beaucoup moins de poissons dans les rivières que dans les lacs contigus. Le climat dur, les variations rapides du niveau de l'eau, les courants rapides, la mauvaise productivité et les accumulations de glace et de frasil nuisent à la présence à l'année longue de communautés nombreuses et diversifiées de poissons. Les espèces trouvées dans ces conditions doivent être capables de s'adapter très facilement et de pouvoir survivre malgré la rareté des ressources alimentaires. Les estuaires, les tronçons aval des rivières et les lacs servent souvent de refuge contre le stress créé par l'hiver dans les environnements marins et lotiques. Les facteurs qui limitent le plus les prises de poissons dans le nord du Québec sont le peu d'abondance du poisson et la teneur élevée en mercure dans les chairs de ce dernier, dans les milieux naturels, mais surtout dans les réservoirs récemment mis en eau et leurs exutoires.

Introduction

Northern Québec is comprised of all watersheds with rivers flowing into James Bay, Hudson Bay, and Ungava Bay, with the exception of a narrow strip of land south of 49°. Since 1971, most of the land south of 55° has belonged to the James Bay Territory, while the rest is still called Nouveau-Québec (Fig. 1).

Northern Québec lies entirely within the Canadian Shield. Its bedrock consists mainly of very old volcanic, metamorphic and igneous rock, with the exception of sedimentary deposits in the Labrador Trench to the east and in the Povungnituk hills to the north. The distribution of surface materials reflects the events following the last ice age (e.g. Flint 1957). On the plateaus where most rivers originate, surface materials consist mainly of thin deposits of moraine

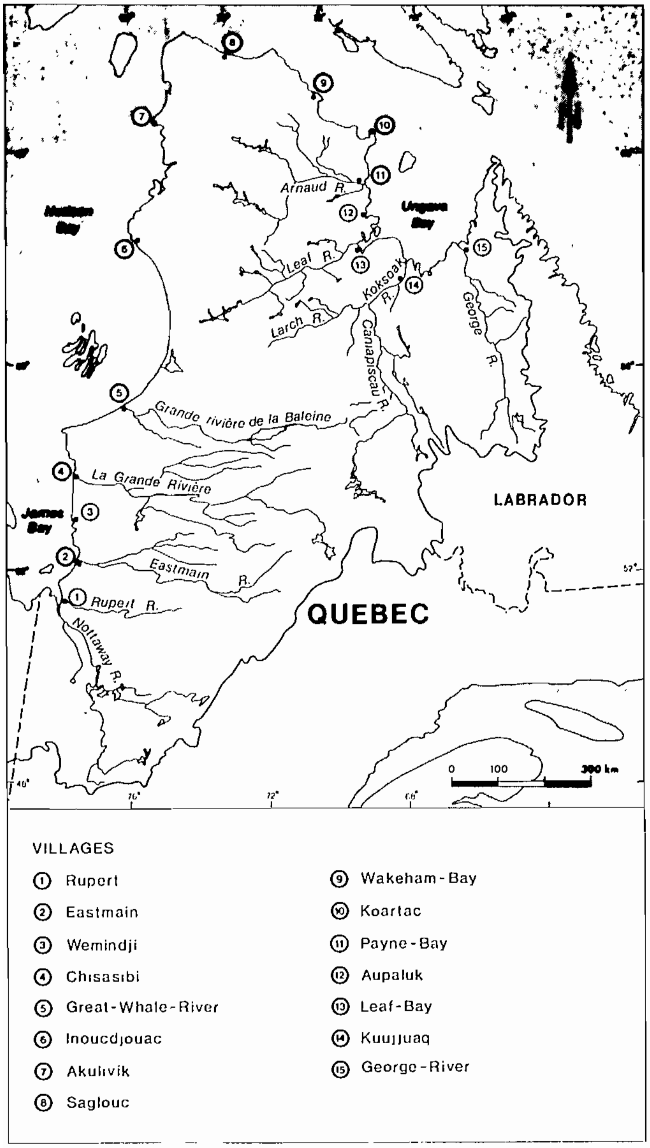

FIG. 1. Main rivers of Northern Québec.

left behind 7000 to 9000 years ago following the glacial retreat. Traces of a few Pleistocene lakes still remain at altitudes of 200 to 300 m, the largest of which is Barlow-Ojibway in the southwest, projecting across the Ontario-Québec border. Lacustrine clay deposits are particularly thick in this area. In the marine environment, deposits of clay, sand and organic matter derived from peat bogs, have accumulated over the moraine at altitudes below 200 m and occasionally 300 m; these deposits may be several dozen metres thick near the sea coast (Fig. 2).

The 72 Québec rivers contribute 39 % of the freshwater flow to James and Hudson bays (8790 $m^3 \cdot s^{-1}$) although they drain only 16 % of their watersheds (Prinsenberg 1977). Eastward, another 39 rivers drain almost 202 000 km^2 and discharge 3500 $m^3 \cdot s^{-1}$ to Ungava Bay (Fig. 1). A few of these rivers and their tributaries (Caniapiscau, Larch), are among the largest rivers in Canada, draining watersheds in excess of 40 000 km^2 (Québec Department of the Environment 1983; Table 1).

Rivers of northern Québec have a young profile (Fig. 3). For example the slope of La Grande Rivière prior to 1979 is virtually constant from the plateau region (500–800 m) to the mouth. The entire river is eroding and has few sedimentation zones due to the high current velocities, the formation of ice in winter and the isostatic rise of the land, the effects of which are seen mainly near the coast. Most of the sediment generated before the last ice age has been removed from the area by advancing ice. As the glacier retreated, it left behind a poorly defined hydrographic system, particularly in the plateau region where lakes intermingle with small rivers (SEBJ 1978).

The climate of northern Québec is continental, except near the sea coast during the open water season. From December to June, bays are almost completely ice-covered and have little effect on the climate. Mean annual temperatures range from 0°C at 49°N latitude to -9°C north of the Ungava peninsula (62°N). The mean for the La Grande Rivière basin is -3°C and varies from -4°C south of the Caniapiscau River to -6°C to the north, near the confluence with the Koksoak River. Accordingly, there is an average of 80 ice-free days in the La Grande Rivière basin, and 60 days in the Caniapiscau River basin (SEBJ 1978).

The water quality of La Grande Rivière in winter and summer has been examined intensively from 1973 to 1984. Table 2 shows the original values of some of the parameters measured before the construction of the power stations. Some 400 km upstream of the river mouth, the water has

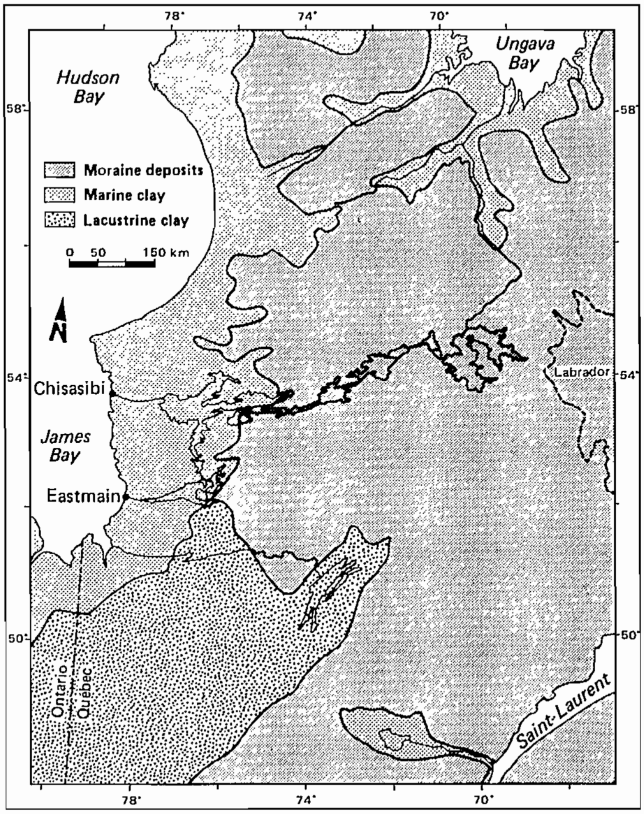

FIG. 2. Main surface material of Northern Québec.

TABLE 1. Annual discharge and specific flow rates of the tributaries of James Bay, Hudson Bay and Ungava Bay, the watersheds of which had pre-1979 surface areas of more than 40 000 km^2.

River (km^2)	Watershed (km^2)	Annual discharge (m^3•s^{-1})	Specific flow rates (L•s^{-1}•km^{-2})
Koksoak	137 011	2438	18
Caniapiscau	89 610	1713	19
Larch	42 735	642	15
La Grande Rivière	97 643	1708	17
Nottaway	65 786	1170	17
Payne (Arnaud)	49 469	633	13
Eastmain	46 361	937	20
Rupert	43 253	907	21
Great Whale River	42 735	646	15
Leaf	42 476	578	14
George	41 699	980	23.5

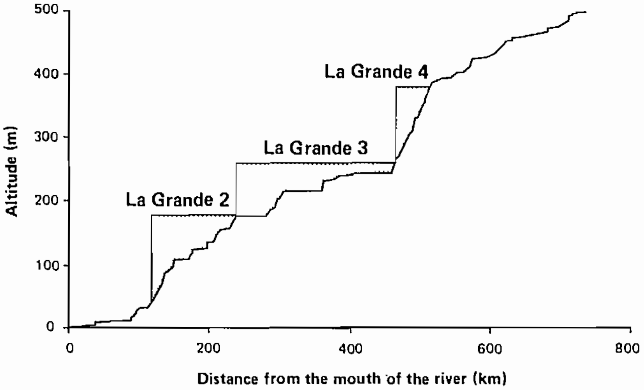

FIG. 3. River profile of La Grande Rivière with and without reservoirs.

TABLE 2. Means and standard deviations (in parentheses) of the water quality parameters observed in La Grande Rivière (1974–78) and the Caniapiscau River (1974–81) before construction of the hydroelectric power projects.

	La Grande Rivière		Caniapiscau
	Downstream	Upstream	Downstream
Number of samples	58	28	19
Color (Hazen units)	23 (4)	19 (16)	13 (5)
Turbidity (NTU)	1.8 (1.2)	0.7 (0.3)	1.2 (0.5)
Maximum temperature (°C)	16.5	18.5	16
O_2 saturation (%)	99 (5)	94 (5)	105 (3)
Conductivity (μS•cm^{-1})	16 (2)	11 (2)	33 (13)
pH (units)	6.4 (0.2)	6.2 (0.3)	7.1 (0.1)
Chlorides (mg•L^{-1})	0.6 (0.3)	0.3 (0.2)	0.5 (0.2)
Bicarbonates (mg•L^{-1})	4.8 (1.4)	2.9 (1.5)	14.0 (5.8)
Sulfates (mg•L^{-1})	2.4 (0.8)	1.4 (0.6)	2.2 (0.9)
Sodium (mg•L^{-1})	0.9 (0.2)	0.5 (0.1)	0.6 (0.1)
Potassium (mg•L^{-1})	0.4 (0.1)	0.3 (0.1)	0.3 (0.1)
Magnesium (mg•L^{-1})	0.3 (0.1)	0.3 (0.1)	1.2 (0.4)
Calcium (mg•L^{-1})	1.3 (0.3)	0.9 (0.3)	3.2 (0.7)
Iron (mg•L^{-1})	0.17 (0.11)	0.08 (0.06)	0.09 (0.03)
Nitrates and nitrites (mg•L^{-1}N)	<0.02	<0.02	0.02 (0.01)
Kjeldahl nitrogen (mg•L^{-1})	0.15 (0.06)	0.11 (0.05)	0.12 (0.03)
Total phosphorus (μg•L^{-1})	8 (4)	5 (1)	5 (1)
Total inorganic carbon (mg•L^{-1})	0.9 (0.4)	1.1 (0.5)	3.5 (1.4)
Total organic carbon (mg•L^{-1})	5.6 (1.1)	4.4 (0.1)	4.0 (1.1)
Silica (mg•L^{-1})	2.6 (0.6)	1.8 (0.6)	1.2 (0.6)
Chlorophyll (μg•L^{-1})	1.28 (0.57)	1.09 (0.54)	0.57 (0.46)

a low dissolved mineral content and little color, is slightly acid and nutrient-poor. The low solubility of the substrate (granite and gneiss) and of the moraine resulting from its abrasion, accounts for these low concentrations. A slight enrichment occurs downstream where the conductivity of the water increases from 11 μS•cm^{-1}, 400 km from the mouth, to 16 or 17 μS•cm^{-1} near the mouth.

The Caniapiscau and Koksoak rivers have only been studied regularly since 1980. However, the 100 observations (approximately) available from 1973 to 1978 show values similar to those in Table 2. The quality of the water in the upstream section of the Caniapiscau River (450 km from the mouth) is similar to that in the upstream portion of La Grande Rivière, since these two waterways originate in the same geological region. Downstream enrichment is barely perceptible up to the inflow of the Swampy Bay River, a major tributary that drains the Labrador Trench, but downstream, enrichment is heightened due to the effect of leaching of marine clay. Accordingly, the Koksoak, which is joined by the Caniapiscau and Larch rivers, contains clear, neutral and relatively rich water (Table 2). This water is, nevertheless, nutrient-poor compared to that of the rivers in central Canada (Bodaly et al. 1989), the Fraser River (Northcote and Larkin 1989), the St. Lawrence River (Edwards et al. 1989) and the rivers in northeastern Ontario (Brousseau and Goodchild 1989).

Most large rivers in northern Québec have been sampled only sporadically. Information gleaned from numerous company reports serves to characterize the rivers by geological region. South of the Rupert River, the water quality of the rivers fall between that of La Grande Rivière and the Moose River (Brousseau and Goodchild 1989). The water quality of the rivers on the eastern shore of James Bay and Hudson Bay north of the Eastmain River and on the western shore of Ungava Bay is similar to that of La Grande Rivière. Finally, the water in the rivers at the southern end of Ungava Bay is similar to that of the Koksoak River.

The number of fish species found in the lakes and rivers declines as one moves northward (Table 3). The species dependent upon extinct Pleistocene lakes such as mooneye (*Hiodon tergisus*), goldeye (*Hiodon alosoides*) and sauger (*Stizostedion canadense*), are not generally found outside the boundaries of Lake Barlow–Ojibway (Ryder et al. 1964; Magnin 1977). Other fish species such as the walleye (*Stizostedion vitreum vitreum*), lake sturgeon (*Acipenser fulvescens*), yellow perch (*Perca flavescens*) and most of the

TABLE 3. List of fish species found within the watersheds of the following rivers: Nottaway (N), Rupert (R), La Grande Rivière (LG), Caniapiscau (C) and Payne (P).

Name	N	R	LG	C	P
Lake sturgeon (*Acipenser fulvescens*)	+	+	+	−	−
Atlantic salmon (*Salmo salar*)	−	−	−	+	−
Brook trout (*Salvelinus fontinalis*)	+	+	+	+	+
Lake trout (*Salvelinus namaycush*)	+	+	+	+	+
Arctic char (*Salvelinus alpinus*)	−	−	−	+	+
Lake whitefish (*Coregonus clupeaformis*)	+	+	+	+	−
Cisco (*Coregonus artedii*)	+	+	+	+	−
Round whitefish (*Prosopium cylindraceum*)	−	+	+	+	−
Goldeye (*Hiodon alosoides*)	+	−	−	−	−
Mooneye (*Hiodon tergisus*)	+	−	−	−	−
Northern pike (*Esox lucius*)	+	+	+	+	+
Lake Chub (*Couesius plumbeus*)	+	+	+	+	−
Emerald shiner (*Notropis atherinoides*)	+	−	+	−	−
Spottail shiner (*Notropis hudsonius*)	+	−	+	−	−
Longnose dace (*Rhinichthys cataractae*)	+	+	+	+	−
Creek chub (*Semotilus atromaculatus*)	−	+	−	+	−
Fallfish (*Semotilus corporalis*)	+	+	−	−	−
Pearl dace (*Semotilus margarita*)	+	+	+	−	−
Longnose sucker (*Catostomus catostomus*)	+	+	+	+	−
White sucker (*Catostomus commersoni*)	+	+	+	+	−
Burbot (*Lota lota*)	+	+	+	+	−
Brook stickleback (*Culaea inconstans*)	+	+	+	−	−
Threespine stickleback (*Gasterosteus aculeatus*)	+	+	+	+	+

cyprinids are not generally found north of La Grande Rivière. Cisco (*Coregonus artedii*), Atlantic salmon (*Salmo salar*), northern pike (*Esox lucius*), lake whitefish (*Coregonus clupeaformis*), round whitefish (*Prosopium cylindraceum*), longnose sucker (*Catostomus catostomus*), and white sucker (*Catostomus commersoni*) all penetrate farther north but only the Arctic char (*Salvelinus alpinus*) and occasionally, lake trout (*Salvelinus namaycush*), are the major river species at the time of migration.

Several hydroelectric power projects affecting northern Québec rivers were studied. The largest include the Complexe La Grande on the river of the same name, the Complexe NBR on the Nottaway, Broadback and Rupert rivers, the Complexe Grande Baleine on the Great Whale River, and the Complexe KCM, the dams of which are mainly on the Koksoak and Caniapiscau rivers. The first phase of the Complexe La Grande was completed in 1985. It involves the construction of three powerhouses — La Grande 2, La Grande 3, and La Grande 4 — each annexed to a reservoir of the same name (Fig. 4). In order to increase the capacity of these stations, 90 % of the discharge of the Eastmain River (810 $m^3 \cdot s^{-1}$) and 45 % of that in the Caniapiscau River (776 $m^3 \cdot s^{-1}$) was diverted to La Grande Rivière. The discharge of La Grande Rivière thus almost doubled at its mouth. Total hydro generation stands at 10 282 MW, derived from a combined surface area for the five principal reservoirs of 11 345 km^2.

There remains, therefore, only 300 km upstream of La Grande 4 and just over 110 km downstream of La Grande 2, within La Grande Rivière as actual river habitat, the rest being a continuous succession of three reservoirs (Fig. 3).

Despite major changes observed in the water quality and fauna of reservoirs during early years of plant operation, water quality downstream of La Grande 2 has remained quite stable (Schetagne and Roy 1985). Table 4 compares the main parameters in the fourth and sixth years after the filling of La Grande 2 with the initial conditions of La Grande Rivière. The greatest long-term change was the drop in summer temperatures downstream from La Grande 2; the water is now as cold as James Bay in summer, but is still warmer in winter (Schetagne and Roy 1985). In the short and middle terms, the increase in mercury content of fish in reservoirs and in river sections downstream of reservoirs will discourage the fishing on a regular basis of the relatively high standing stocks of these environments (Messier et al. 1985).

History of Commercial Fishes

Initial observations of river fishes were geared to exploring the possibility of building commercial fisheries in the estuaries of the main rivers flowing into James Bay and Hudson Bay (Lower 1915; Melvill 1915; Halkett 1919). However, fish populations proved to be small, grew slowly and consisted mainly of old individuals. Populations, with the exception of Arctic char, could not withstand commercial fishing in addition to subsistence fishing, even when caution was exercised (Huntsman 1931; Dymond 1933, 1941; Vladykov 1933; Hunter 1968). The same was true for fish in tributaries of Ungava Bay, where Atlantic salmon occur (Dunbar and Hildebrand 1952; Le Jeune 1967; Power 1969).

Quotas of 14 000 kg for Arctic char were set for large rivers in the early 1960's. Ten years later, fish yields and mean sizes had declined so much at each fishing site that all fisheries ceased (Gillis et al. 1982). Atlantic salmon fishing halted between 1930 and 1960, but resumed at Kujjuaq and continues today. The quota deemed safest for this species in the Koksoak River, the most productive river, is 18 000 kg which includes both commercial and subsistence fishing. Few Atlantic salmon commercial fisheries operate in other northern rivers where this species is found.

Meanwhile, exploratory expeditions were conducted in large lakes of the southern James Bay watershed. These include, among others, the work carried out or reported by Dymond and Hart (1927), Bajkov (1928), Richardson (1944), Radforth (1944), Legendre and Rousseau (1949), McAllister and Bleakney (1958), Legendre (1962a, 1962b), Ryder et al. (1964), Beaulieu and Corbeil (1964), Le Jeune (1964a, b, 1965), Magnin and Legendre (1964), and Le Jeune and Faucher (1972). At least for Québec, this work enabled commercial fisheries to be established for lake sturgeon, walleye, northern pike, lake trout and lake whitefish, as well as for collecting brook trout (*Salvelinus fontinalis*) spawners and eggs. Most fisheries were forced to cease operations due to the vulnerability of the stocks (lake sturgeon), the excessive rate of parasitism in fish flesh (lake whitefish in Mistassini Lake), or an excessive level of mercury in the flesh, even in certain pristine regions (lake trout, walleye, northern pike).

Interest was less intense in inland river sections and focused solely on continuing the studies already in progress on anadromous fish populations (Power and Oliver 1961; Power 1969; Jessop et al. 1970) and lake sturgeon (Magnin 1964, 1965, 1966).

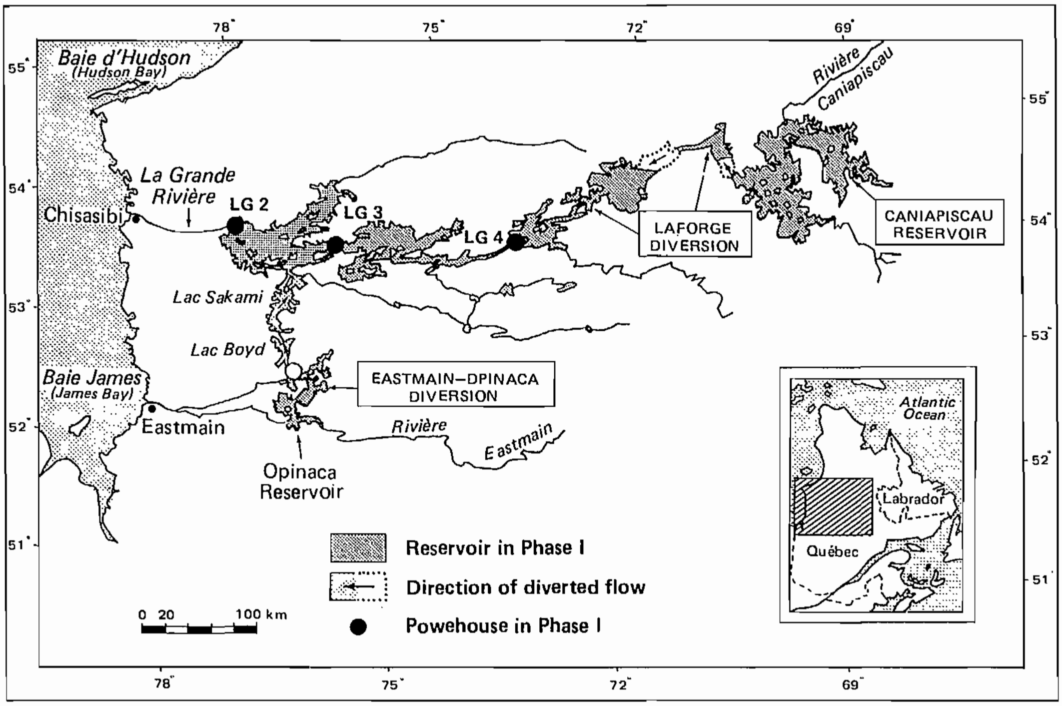

FIG. 4. La Grande Complex.

TABLE 4. Means and standard deviations (in parentheses) of the water quality parameters observed at the mouth of La Grande Riviere before (1974–78) and after the flooding of the La Grande 2 reservoir (1979).

	1974–78	1982	1984
Number of samples	58	13	11
Color (Hazen units)	23 (4)	27 (5)	24 (2)
Turbidity (NTU)	1.8 (1.2)	2.0 (1.6)	1.5 (1.1)
Maximum temperature (°C)	16.5	10	12
O$_2$ saturation (%)	99 (5)	95 (3)	96 (4)
Conductivity (μS•cm^{-1})	15.6 (2.3)	16.4 (0.7)	13.7 (0.7)
pH (units)	6.4 (0.2)	6.3 (0.1)	6.4 (0.1)
Chlorides (mg•L^{-1})	0.6 (0.3)	0.6 (0.1)	0.4 (0.1)
Bicarbonates (mg•L^{-1})	4.8 (1.4)	4.3 (0.4)	3.4 (0.1)
Sulfates (mg•L^{-1})	2.4 (0.8)	1.5 (0.7)	1.6 (0.2)
Sodium (mg•L^{-1})	0.9 (0.2)	0.9 (0.2)	0.8 (0.2)
Potassium (mg•L^{-1})	0.4 (0.1)	0.6 (0.1)	0.4 (0.1)
Magnesium (mg•L^{-1})	0.3 (0.1)	0.5 (0.1)	0.3 (0.1)
Calcium (mg•L^{-1})	1.3 (0.3)	1.5 (0.3)	1.2 (0.3)
Iron (mg•L^{-1})	0.17 (0.11)	0.20 (0.10)	0.20 (0.10)
Nitrates and nitrites (mg•L^{-1}N)	<0.02	0.04 (0.02)	0.03 (0.01)
Kjeldahl nitrogen (mg•L^{-1})	0.15 (0.06)	0.16 (0.02)	0.16 (0.02)
Total phosphorus (μg•L^{-1})	8 (4)	15 (6)	12 (3)
Total inorganic carbon (mg•L^{-1})	0.9 (0.4)	1.9 (0.3)	1.4 (0.2)
Total organic carbon (mg•L^{-1})	5.6 (1.1)	5.3 (0.6)	5.3 (0.6)
Silica (mg•L^{-1})	2.6 (0.6)	1.3 (0.5)	1.1 (0.3)
Chlorophyll (μg•L^{-1})	1.28 (0.57)	1.40 (1.15)	1.74 (0.86)

Sport and Subsistence Fishing

In northern Québec some 100 000 people subsist on agriculture, forestry and mining. Sport fishing, the yield of which is not precisely known, is confined mainly to lakes, and the principal species caught are walleye and northern pike. North of 50°N, there are only some 20 000 inhabitants, approximately 10 000 of which are Indians and, north of 55°N, 5000 Inuit. The others are of European derivation who provide services or work in the few operational mines. The number of workers employed in building hydroelectric projects ranged from a few hundred in 1973 to 17 000 in 1978 but numbers fell to less than a thousand by the end of 1984. Workers did not have suitable vehicles for travelling to remote sites. These workers have had a minimal impact on fishing populations except in the vicinity of the work sites.

Northern Québec natives have been guaranteed the right to priority usage of wildlife resources. A study was conducted among all bands in order to determine present requirements. Harvesting levels for 1972 to 1980 are now known (Native Harvesting Research Committee 1982, in preparation). Data on harvest levels has already been compiled, except for small areas (Weinstein 1976; Gillis and Kemp 1983; Berkes 1985).

Native Cree bands mainly use the territory south of 55°N. Three Cree bands hunt inland throughout the year; fishing is done in lakes and, but rarely, in rivers. Depending on availability of resources and requirements of trapping activities, bands established at the mouth of rivers concentrate their activities along shores (spring, autumn) or inland (winter, summer). Fish harvests reflect this lifestyle; white-

TABLE 5. Mean annual biomass (kg) of fish caught over a five year period by Cree Indians and Inuit. These data include their subsistence requirements plus a few commercial fisheries.

Species	Cree	Inuit	Total
Lake sturgeon	7 080	—	7 080
Atlantic salmon	—	30 640	30 640
Brook trout	11 990	15 770	27 760
Lake trout	16 930	71 520	88 450
Arctic char	570	201 990	202 560
Whitefish (including cisco)	45 520	12 810	58 330
Northern pike	14 130	—	14 130
Suckers (longnose and white)	16 110	—	16 100
Burbot	2 860	—	2 860
Walleye	5 510	—	5 510
Cod (Ogac)	—	8 060	8 060
Sculpins and eel pouts	—	2 860	2 860
Total mass	120 700	343 650	464 350

fish and brook trout are caught mainly near James Bay, while northern pike and walleye come from inland lakes. The average annual catch is estimated at 120 700 kg of fish. Whitefishes (lake whitefish, cisco and round whitefish), lake trout, suckers (longnose and white), northern pike and lake trout are, by order of priotity, the species with the largest yields (Table 5).

Inuit fish mainly in the coastal habitats and the strip of land easily accessible from the coast. This is reflected in their fish catch by the abundance of migratory species (Arctic char, Atlantic salmon, brook trout, whitefishes) and marine species such as Greenland cod (*Gadus ogac*) and eelpouts (Zoarcidae). Lake trout and Arctic char are also caught frequently during winter when ice fishing. Inuit take an average of 343-650 kg•yr^{-1}, 59 % of which is Arctic char and 21 % lake trout (Table 5 and 6).

Fish Data

The 1971 announcement of a hydroelectric power project and the formation of a regional government (Société de développement de la Baie James — SDBJ) marked the start of a long series of studies on aquatic and land ecosystems. The importance of rivers as environments for spawning and as nursery areas became apparent. Rivers were also migratory routes for various types of aquatic fauna and its users. River studies subsequently focused mainly on protecting stocks of fish caught by natives, mitigating the effects of the hydroelectric project on La Grande Rivière, and protecting against the spread of undesirable species. The main observations and their conclusions are cited in a synthesis study sponsored by the Biophysical Agreement (SDBJ and Environment Canada 1980) and in numerous reports prepared by or for the Société d'énergie de la Baie James (SEBJ) and Hydro-Québec. The principal reports deal with the ecology of the James Bay Territory (Magnin 1977; SEBJ 1978), and their fish populations (Ministère du Loisir, de la Chasse et de la Pêche (MLCP); Société d'aménagement général de l'environnement (SAGE) 1980a, 1980b, 1981; SAGE 1981; Boucher and Roy 1982, 1985; MLCP et al. 1982; Laramée 1983; Lalumière et al. 1985; SEBJ and SOTRAC 1985; Hydro-Québec and SEBJ 1985). Using these documents and supplementing them with on-site observations, I will attempt to summarize some imporant characteristics of several large rivers of northern Québec.

Fish Abundance

As a prior condition, it is necessary to distinguish between the sections of rivers that do not afford good access due to unfavorable water levels, and those that permit seasonal migrations of fish. Furthermore, a waterway with a high order of 6 or more will be considered to be a large river (Vannote et al. 1980).

Before 1979, the last 600 km of La Grande Rivière and the Eastmain River had all the characteristics of large rivers with limited access due to unfavorable water levels. The Caniapiscau River has the same conditions over the last 500 km of its course, except in the vicinity of Cambrien Lake. In these river sections, standing stocks of fish are lower than in adjacent lakes of 5 km^2 or more (Table 7). Yields per unit of effort are four times lower in the Eastmain River and La Grande Rivière than in the adjacent lakes, and approximately three times lower in the Caniapiscau River

TABLE 6. Yield as number of fish per year and per fisherman caught in each Cree or Inuit village in 1976-77 during a study to determine a harvesting level for native populations.

Village	Number of fishermen	Lake sturgeon	Atlantic salmon	Arctic char	Brook trout	Lake trout	White-fish	Northern pike	Suckers	Burbot	Walleye	Cod	Eelpouts	Total
Rupert	212	0.6	0	0	3.3	0.2	49.7	4.5	7.5	0.2	6.8	—	—	72.8
Eastmain	72	1.7	0	0	33.6	1.0	119.3	7.7	10.9	0.2	11.7	—	—	186.1
Wemindji	140	0.7	0	0	20.0	3.5	118.1	8.6	6.1	0.5	2.7	—	—	160.2
Chisasibi	375	0.8	0	1.1	46.6	9.9	81.8	7.6	22.2	2.2	3.8	—	—	176.0
Great Whale River	168	0	0.6	8.9	60.0	38.5	106.1	10.4	45.9	3.3	0	50.3	60.8	330.8
Inukjuak	112	0	5.2	117.4	16.8	94.0	75.6	—	—	—	0	31.3	7.0	407.3
Akulivik	29	0	0	725.1	0.8	64.5	35.0	—	—	—	0	25.9	8.4	859.7
Saglouc	79	0	0	696.7	0.6	53.6	1.2	—	—	—	0	8.5	15.6	776.2
Wakcham Bay	55	0	0.1	199.0	1.3	13.7	0.1	—	—	—	0	0.6	43.2	258.0
Koartac	31	0	0.5	91.0	0.1	20.9	1.0	—	—	—	0	0	24.6	138.1
Payne Bay	41	0	0.5	322.5	5.5	43.4	1.0	—	—	—	0	0.1	12.5	385.5
Aupaluk	8	0	0.3	299.6	26.9	27.1	0.8	—	—	—	0	0.6	46.3	401.6
Leaf Bay	17	0	1.5	347.5	44.1	31.5	8.4	—	—	—	0	0	82.9	515.9
Kuujjuaq	135	0	60.0	70.6	56.3	38.1	39.5	—	—	—	0	4.6	36.1	305.2
George River	53	0	14.4	555.1	89.7	27.9	94.4	—	—	—	0	2.9	19.2	803.6

TABLE 7. Comparison of fishing yields in rivers and in lakes.

	Complexe La Grande	Caniapiscau watershed
Rivers		
Fishing effort (net•day)	55	25
Number per unit effort (N•net^{-1}•day^{-1})	4.1	17.6
Mass per unit effort (Kg•net^{-1}•day^{-1})	3.8	14.0
Lakes		
Fishing effort (net•day)	68	57
Number per unit effort (N•net^{-1}•day^{-1})	17.4	56.4
Mass per unit effort (kg•net^{-1}•day^{-1})	15.8	38.8
Rivers/lakes yield ratios		
Numerical ratios	0.24	0.31
Mass ratios	0.24	0.36

(SAGE 1981; Boucher and Roy 1985). These observations were made using the standardized fishing gear of nets made of six 8-m-long panels each consisting of 25, 37, 50, 67, 75 and 100 cm stretched mesh. Supplementary fishing with trammel nets, fish traps and fishing rods verified that the species and sizes had not generally been underestimated. This ratio of three or four to one between lake harvests and actual river harvests was found everywhere north of the Rupert River by SEBJ or its consultants, except in long slow sections where fish abundance was closer to that of lakes.

A potential harvest level for these rivers can be estimated based on these observations. Of necessity, this level will be theoretical since the test netting has been limited and sporadic. The mean potential harvest was assessed using a modified morphoedaphic index (Ryder 1965) in order to take into account mean annual air temperature (Schlesinger and Regier 1982). The estimated level was approximately 2.3 kg•ha^{-1}•yr^{-1} for the mean of the lakes in the Eastmain River and La Grande Rivière basins, and in the Caniapiscau River basin, at values ranging from 1.6 to 2.3 kg•ha^{-1}•yr^{-1}, depending on the latitude. Using the river harvest/lake harvest ratio, we obtain a level of 0.5 to 0.6 kg•ha^{-1}•yr^{-1} for the Eastmain River and La Grande Rivière, and of 0.6 to 0.8 kg•ha^{-1}•yr^{-1} for the Caniapiscau River. Less rigorous data we have for rivers further north (Larch, Koksoak, Leaf) suggest lower yields for the resident populations.

Except for rivers flowing into southern James Bay for which we have less data, there are few areas where lake fish have easy access to large rivers. The main areas are Bienville Lake on the Great Whale River, Cambrien Lake on the Caniapiscau River and Lac de la Hutte Indienne on the George River. There is seasonal migration upstream or downstream wherever there are no obstacles. Fish yields in there river sections are similar to, and sometimes even higher than yields in lakes.

Fish also have easy access to the sea near river mouths. Three general types of habitat are found there: river estuary, marine estuary and the freshwater plume.

The river estuary is simply the extension of the river into the range of tidal influence. The length of this section depends mainly on the topography of the banks, the flow rate of the river, the height of tide, the proximity of the first large falls or rapids upstream, and the presence of ice cover. This zone can range from a few kilometres in length, such as in the estuary of the Great Whale River, to some 30 km on the Koksoak River. Water here is fresh all year, so this section harbors species that generally are intolerant of high levels of salinity, (e.g. northern pike and white sucker). Freshwater species that summer in brackish or salt water (brook trout, whitefishes) return to the river estuary to spawn or simply to over-winter. This area is heavily fished during migration and in winter.

Next downstream is the marine estuary marked by the first appearance of brackish water. This section varies in length throughout the year, as in the case of the river estuary, but in the opposite direction. La Grande Rivière had just a small marine estuary before 1979, but since the power stations were built, it no longer exists in winter and is limited in summer. Near Ungava Bay where spring tides can reach 13 m, marine estuaries often measure 50 km (Koksoak River) or even 80 km (Payne River). The salinity of the water there may range from 0 to 28‰ in certain cases. Marine fishes are found, such as the fourhorn sculpin (*Myoxocephalus quadricornis*), as well as some freshwater species that make forays into brackish or salt water. The most common of the latter are the Atlantic salmon, Arctic char, brook trout, cisco, lake whitefish, and longnose sucker. Fish feed in the marine estuary in summer, but avoid the area in winter when only the marine fish are found there (Boucher and Roy 1982). Subsistence fishing is usually done during spring and autumn migrations and in summer.

The freshwater plume is equivalent to the marine estuary except that it is semicircular rather than linear in shape, and the brackish layer is relatively thin (3–5 m) and overlies salt water. The same species previously described are found there with a preponderance of pelagic varieties. The section along the shoreline is used for subsistence fishing, but the offshore area is avoided, as it is rather unproductive. In summer, standing stocks of fishes in the plume and marine estuaries appear similar to those of lakes in the same region. Hunter et al. (1976) calculated that Fort George Cree (Chisasibi), in 1973 and 1974, harvested fish at the rate of 1.95 kg•ha^{-1} when the river portion occupied by anadromous fish in summer is taken into account. This level of harvest was thought to be the maximum allowable level. Berkes and Freeman (1986) estimated the mean harvest rate in the same region at 0.9 kg•ha^{-1}•yr^{-1} between 1973 and 1979. This value reflects the large variations possible for harvests, which in some years were three or four times higher than lowest levels.

The species found in the river estuaries of northen Québec have one characteristic in common, that is, during their life cycle, they reach a stage at which they are vulnerable to seaward movements. This may occur when the larvae are pelagic, such as for the lake whitefish, cisco and longnose sucker. It can also occur at the smolt stage in the Atlantic salmon, Arctic char and brook trout. This propensity to seaward movement can last throughout the life cycle, such as in the cisco. The occurence of a species in the river estuary or freshwater plume depends mainly on feeding habits and thermal preferences. Consequently, cisco, lake whitefish, Arctic char, brook trout and Atlantic salmon form substantial populations since maximum temperatures in James Bay, Hudson Bay and Ungava Bay range from 8 to 12°C (SEBJ

1978), which are close to the preferenda of these species, but which preclude walleye, which prefer higher temperatures.

Distribution of Fish

One characteristic of fish associations encountered in summer in northern environments is the indeterminate separation between freshwater and brackish water communities, and between river and lake communities. In the area south of the territory studied, several species are confined to lake habitats, with the occasional exception of a short period corresponding to the spawning season when they may become adfluvial. Coldwater species, such as lake trout and burbot, are usually restricted to deep lakes and coldwater zones of lakes during summer, while warmwater species, such as northern pike and yellow perch, remain in the warmer stratum of either lakes or rivers. There, the latter species find the same conditions in the rivers as in the surface layers of lakes in summer. Coldwater species avoid rivers in summer since temperatures are too high. This marked preference for lakes has, in southern Canada, caused them to be classified as typically lake species (cisco, lake whitefish, lake trout, lake sturgeon). Moving northward, temperatures fall, the warmwater species are replaced by coldwater species and the lake and river communities become similar. Thus, in the Eastmain River basin, lake sturgeon are more often found in rivers throughout the year. Lake whitefish are widespread in rivers from the Rupert River to north of Inukjuak. Cisco, a pelagic species, are carried downstream in rivers and into estuaries. Even lake trout, often reputed to be a deepwater species, will be abundant wherever current velocities are not excessive, even in shallow river sections, a clue perhaps, that temperature rather than depth per se, determines their location.

Factors Causing Low Productivity in Large Northern Rivers

Environmental stability and food abundance are the most important factors in determining fish production of large rivers in northern Québec. The physical environment is generally more stable in lakes than in rivers. Water volumes, levels and surface areas fluctuate according to seasonal flows, and the range of these modifications in rivers vastly exceeds that of lakes. Currents and turbulence only rarely limit fish production in lakes, but these factors may seriously shrink the occupiable habitat of large rivers depending on fish species in question. The northern environment can exacerbate two stream phenomena, those of seasonal distribution of water flow and effects of ice accumulation.

As we move northward in Québec, precipitation is not only substantially less but much of it accumulates as snow or ice. During winter, water from lakes and seepage water does not maintain a strong flow in rivers. In less than a month, the resulting low water level are usually followed by very heavy spring flooding. For example, the Nottaway River has an average ratio of 10:1 between the maximum daily flood and the minimum winter discharge; over the last 20 years, this ratio of the recorded maximum and minimum discharges exceeded 25:1 (Fig. 5). On the other hand, the Larch River, a major tributary of the Koksoak River, recorded a ratio of 125:1 for flows measured in 1981–82 and of 325:1 for the period between 1963 and 1982 (Québec Department of the Environment 1983). These two hydrograms also show that variations in summer flow rates are more irregular in the north due to low water retention capacity of soils at that time of year. This situation differs from that on the Mackenzie and Churchill rivers where the variations in flow rate between the winter low water and the spring flood level are only in order of 1.5:1 to 2:1 (Bodaly et al. 1989).

Turbulence causes rapids to freeze slowly; consequently, large quantities of ice and frazil are generated, occasionally over a period of 5–6 months. These ice crystals accumulate under the stable ice layer and pile up to form suspended dams. One of these reached a thickness of almost 50 m near the La Grande 4 site. In shallow rivers with a rough bottom, frazil attaches the stones on the river bed and forms anchor ice. If both types occur simultaneously, ice dams are formed and partially block the flow of water. Carter (1978) working at the Gorge d'en Haut on the Caniapiscau River estimated that the volume of ice accumulated over a maximum distance of 10 km was 41 250 000 m^3. When flood waters arrived, anything that had not been eroded was carried away by the current, the bottom was scraped, and materials from the banks moved to heights of more than 10 m above the mean level of the river. Since the Complexe La Grande became operational, many of these ice accumulation sites have been lost due to the inundation of rapids or as a result of reduced flow, thereby enabling an ice cover to form more rapidly. On the other hand, a few accumulation sites have appeared along diversion paths, but new volumes are vastly lower than those recorded for the rivers as a whole. The ice accumulation phenomenon in small and large rivers is probably the cause of fish leaving many sections of these waterways in winter for preferred sites in rivers or adjacent lakes (Power 1966).

Slight variations in pH, dissolved salt concentrations and turbidity are observed during snowmelt and spring leaching of soils (Tables 2 and 4). These differences are not sufficient to explain why the numbers and mass of fish in rivers are lower than in lakes.

Despite nutrient concentrations at least equal to those of adjacent lakes, phytoplankton production is relatively low in rivers. Tseeb (1962) holds that phytoplankton production can only occur normally if the current velocity is less than 0.2 m•s^{-1}, which is usually exceeded in the large rivers of northern Québec. Periphyton may occupy shallow areas, but is limited by depth of the river and subsurface illumination. In this respect, La Grande Rivière is doubly disadvantaged by mean current velocities of the order of 1 m•s^{-1} and depths often in excess of 5 m. Despite current velocities of the same order of magnitude, the Larch River and its main tributaries are shallow, and periphytic production is abundant. This is likely one of the factors that favor a relatively high density of young Atlantic salmon produced by these tributaries of the Koksoak River. In this regard, the Larch River has several characteristics in common with the Moisie River (Sedell et al. 1989) and the Miramichi River (Randall et al. 1989).

Rivers receive zooplankton from the surface water of lakes. Since this stratum is fairly poor in individuals, contributions to rivers are minimal. In La Grande Rivière and the Caniapiscau River, summer biomasses rarely exceed

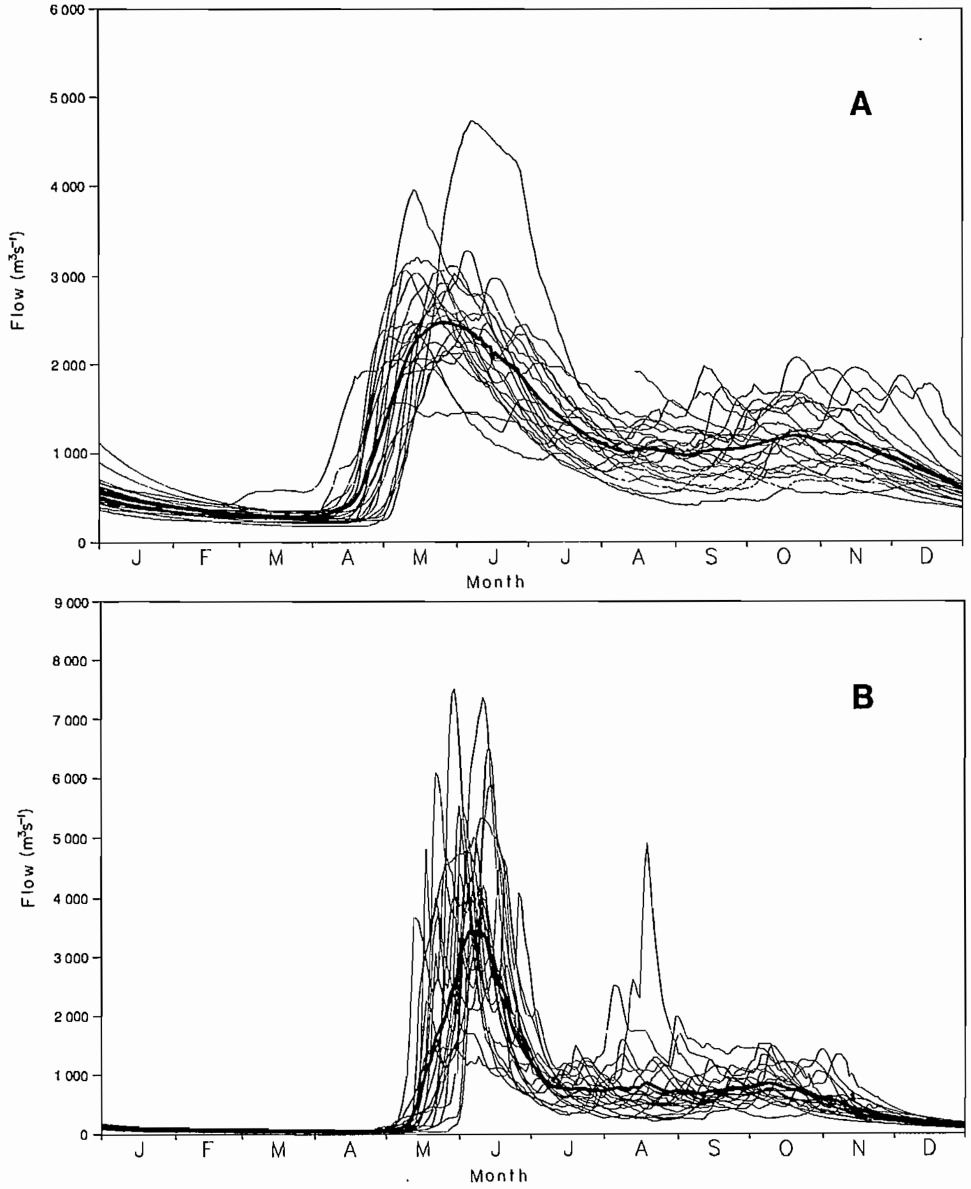

FIG. 5. Hydrograms of the Nottaway (A) and Larch (B) rivers.

1 mg•L^{-1}, even at highest production levels. During the same period, biomasses remain at 20–70 mg•L^{-1} in lakes. Downstream from reservoirs, this biomass may reach up to 8 mg•L^{-1}, although the usual level is 2 mg•L^{-1}; this differential is due to the position of water supply points at the thermocline level (Roy 1985). The residence time of water in rivers is less than or equal to the duration of one generation of rotifers or cladocerans, and thus prevents these organisms from establishing populations. Copepods encounter more constraints since the life cycle of the species found is usually one year. In high-water periods, littoral zone species may temporarily form rich concentrations in sheltered bays and floodplains, but only for a short time. As soon as the water returns to the main stem of the river, this potential source of food for alevins and young fish is no longer available. Since the duration of these floods is shorter in northern Québec rivers and the period in which they occur varies from year to year, floodplains, used heavily in the south, become increasingly rare as one moves northward.

Except in the rare sedimentation zones of rivers where concentrations of oligochaetes and small pelecypods develop, benthic fauna consists almost exclusively of insect larvae and nymphs, diptera being the most abundant and ephemeroptera, trichoptera and plecoptera having the greatest biomass (Boudreault and Roy 1985). Gastropods and amphipods are not abundant due to the lack of shelter, low calcium content and low water temperatures. Rivers are generally equal or less rich in insects than lakes.

Most large rivers in northern Québec are not good permanent habitats for fish. The austere conditions caused by rapidly fluctuating water levels, the formation of abundant frazil and low levels of primary production restrict the year-long maintenance of abundant and diversified fish communities. Some individuals that are relatively undemanding in terms of food, may spend the summer in this environment and, since they are few in number have growth rates and condition coefficients comparable to those of the adjacent lakes. North of 55°, the main use of rivers are migration corridors and wintering refuges for adfluvial or anadromous fishes or as inland migratory routes between lake environments.

Dispersion of Fish

After the original dispersion from refugia in the Mississippi and the Atlantic via postglacial lakes, temporary interconnections between rivers and brackish waters of the coastlines allowed species to reach lakes, either downstream or upstream. Upstream dispersion depended on the swimming ability of the species, the poor swimmers (e.g. cisco) remaining close to the Pleistocene lakes or former marine submergence, and the better swimmers moving upstream as appropriate habitats became available. Downstream dispersion occurred simultaneously with the isostatic rise of the land and the retreat of salt water, and was likely followed by the seaward movement of larvae or young fish.

The same factors that affected the abundance of fish determined the distribution of the species. The winter period with all of its constraints such as severely low water levels, low temperatures (0°C), ice cover, frazil formation, and prolonged fasting, increases at higher latitudes. The ability to exploit rapidly available food during a very short period of the year, and optimize this energy source through specific behaviour patterns, enables some species to survive more easily than others under these austere conditions. Percidae and Esocidae, usually considered to be coolwater fishes, become scarce first, followed by Coregoninae and finally Salmoninae (Table 3). This order of presence is the same as that linked to the eutrophy–oligotrophy gradient, since the food abundance during the year seems to be the governing factor. By analogy, if most of the lakes in Québec north of 50° may be termed oligotrophic, the rivers would then be ultraoligotrophic from a biological standpoint.

The order of species presence or absence and of the reduction in biomass of river residents, is similar to that of their phenotypic plasticity and hence adaptability to variable environmental conditions. Lindsey and Woods (1970) suggested that various forms of ciscos and whitefishes were determined according to habitat preferenda and postglacial dispersion. The Atlantic salmon of the Koksoak River basin, at its northern limit of distribution, also clearly illustrates this strong ability to adjust to adverse conditions. Within a single population, all intermediaries between landlocked, estuarine and marine forms are found. There are even cases of individuals returning from the sea that will not spawn until the following year, and other cases in which individuals have returned to fresh water and spawned twice without returning to the sea (Power 1969; MLCP and SAGE 1980a; MLCP et al. 1982). This phenotypic diversity of form and behaviour enables the species present to withstand the wide variability in climate found in these areas, particularly in rivers. Consequently, the relative stability of a species must be assessed on a longer time scale than normally used for rivers farther south.

Fish species normally confined to freshwaters in the southern part of Québec, become anadromous in the northern regions. These species include cisco, lake whitefish, brook trout, longnose sucker and, farthest north, the Arctic char. These fishes live in fresh water, but feed mainly in the plumes of rivers, where salinity is 15–25 ‰ or less, depending on the species. In order to avoid the low temperatures of brackish waters in winter, fish of all ages return to the fresh water of the river estuaries and adjacent lakes either to spawn or overwinter (Morin et al. 1980; Boucher et al. 1984). This behaviour is exhibited farther south by the brook trout and Arctic char, but occurs in other species only in more northern areas. The routine ocean migration of Atlantic salmon is an extreme example of similar behaviour. Since most of the Atlantic ocean has favorable temperatures in winter, salmon are not obliged to overwinter in fresh water; instead, they initiate the return migration to the river of origin according to their state of maturity.

The size of migrating fish populations depends upon the number of young fish generated from the accessible freshwater environments (lakes, rivers, streams), on the length of the river outflow zone and on food abundance. On the eastern shores of James Bay and Hudson Bay, the availability of food in the plume is comparable to that of the richest lakes in the region. This level is nevertheless very low, and returning fishes have a great impact on the limited resources (Messier et al. 1986). For example, the annual yield of fish migrating to La Grande Rivière was of the order of 50 t and the mean flow rate of the river was 1700 $m^3 \cdot s^{-1}$. The Fraser River, with a flow rate 5–6 times higher, supports migrations estimated in terms of tens of thousands of tonnes (Northcote and Larkin 1989). This clearly shows the paucity of nutrients in La Grande Rivière, which generates young fish, and of its estuary and outflow zone, which provide the food required by older fish migrating upstream from James Bay.

Conclusion

The aquatic environments of northern Québec are unproductive due to the paucity of dissolved nutrients and the austere and rigorous nature of the climate. Wide variations in discharges and current velocities plus the formation of frazil, further hinder the development of large standing stocks of fishes in the typical river seetions. The species found therein have pioneering qualities such as phenotypic plasticity and adaptability, and a high potential for persistence and readjustment following sudden changes. Rivers, estuaries and lakes most often provide refugia from the rigors of winter in both marine and freshwater environments although, in the latter case, lakes are preferred.

Native people derive a large proportion of their total wildlife harvest from fish. Inland lakes usually meet their needs but, in coastal regions, anadromous fish account for a large proportion of their subsistence fishing.

Some conclusions that can be made after more than 10 years of study and monitoring in northern Quebec are:

> An overview of the largest lakes north of the 55th parallel, provides an indication of the relative abundance of species in the rivers at the same latitude; extensive river sampling would be necessary to increase the level of precision of standing stock estimates, even slightly.
>
> Determination of fish yield potential in northern rivers may be accomplished through the use of aerial photographs. Reconnaissance at the start of the thaw in regions

where there were numerous rapids which could generate large volumes of ice, would provide the best information pertaining to the most extreme conditions encountered.

Some forms or varieties of fishes can differ from one watershed to another, or within the same watershed. In these instances, stock determination is paramount, and desirable stocks such as the Assinica brook trout should be protected, at least until their status is determined.

Finally, because of the heavy use of anadromous fish stocks by native peoples, an appropriate level of regulation is required. We still have much to learn about major stocks, such as their distribution in freshwater outflow zones, at various depths and salinity levels. It would be advisable to make use of the resource developers' user-based approach, which has the facility of producing volumes of data at relatively little cost.

References

Bajkov, A. 1928. A preliminary report on the fishes of the Hudson Bay drainage system. Can. Field-Nat. 42: 96–99.

Beaulieu, G., et E. Corbeil. 1964. Étude préliminaire de l'esturgeon de lac (*Acipenser fulvescens*) dans la région de l'Abitibi. Naturaliste can. 91: 175–181.

Berkes, F. 1985. Resource harvesting, land use and access in the area downstream from LG 2. For the Chisasibi Band Council, Chisasibi, Québec. 56 p.

Berkes, F., and M. M. R. Freeman. 1986. Human ecology and resource use, p. 425–455. *In* I. P. Martini [ed.] Canadian Inland Seas. Elsevier Science Publishers.

Bodaly, R. A., J. D. Reist, D. M. Rosenberg, P. J. McCart, and R. E. Hecky. 1989. Arctic rivers: fish and fisheries of the Mackenzie and Churchill Rivers, p. 128–144. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Boucher, R., et D. Roy. 1982. Les conséquences de la coupure de La Grande Rivière sur les poissons en aval du réservoir de LG 2. Direction Environnement, Société d'énergie de la Baie James, Montréal. 44 p.

1985. Poissons. *In* Réseau de surveillance écologique du Complexe La Grande 1978–1984. Direction Ingénierie et Environnement, Société d'énergie de la Baie James, Montréal, Québec. 119 p.

Boucher, R., P. Wickham, et D. Roy. 1984. Modifications observées sur La Grande Rivière en aval du réservoir de LG 2. Direction Ingénierie et Environnement, Société d'énergie de la Baie James, Montréal, Québec 104 p.

Boudreault, J., et D. Roy. 1985. Macroinvertébrés benthiques. *In*: Réseau de surveillance écologique du Complexe La Grande 1978–1984. Direction Ingénierie et Environnement, Société d'énergie de la Baie James, Montréal, Québec. 102 p.

Brousseau, C. S., and G. A. Goodchild. 1989. Fisheries and yields in The Moose River Basin, Ontario, p. 145-158. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Carter, D. 1978. Troncon inférieur de la rivière Caniapiscau: hydrologie, hydraulique, glaces, transport solide. Rapport présenté au Groupe d'étude conjoint Caniapiscau–Koksoak, Montréal, Québec. 104 p.

Dunbar, M. J., and H. H. Hildebrand. 1952. Contribution to the study of the fishes of Ungava Bay. J. Fish. Res. Board. Can. 9: 83–128.

Edwards, C. J., P. L. Hudson, W. G. Duffy, S. J. Nepszy, C. B. McNabb, R. C. Haas, C. R. Liston, B. Manny, and W.-D. Busch. 1989. Hydrological, morphological and biological characteristics of the connecting rivers of the international Great Lakes: a review, p. 240-264. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Dymond, J. R. 1933. Biological and oceanographic conditions in Hudson Bay. Contr. Can. Biol. N. S. 8: 1-12.

1941. Atlantic salmon in Ungava Bay. Can. Field-Nat. 55: 19–20.

Dymond, J. R., and J. L. Hart. 1927. The fishes of Lake Abitibi (Ontario) and adjacent waters. University of Toronto, Publ.Ont. Fish. Res. Lab. 28: 1–19.

Flint, R. F. 1957. Glacial and Pleistocene geology, John Wiley & Sons, Inc., New York, NY.

Gillis, D. J., M. Allard, and W. B. Kemp. 1982. Life history and present status of anadromous arctic char (*Salvelinus alpinus* L.) in Northern Quebec with case studies on the George, Payne and Kovik Rivers. Presented to Kativik Regional Government. Kuujjuaq, Quebec. 107 p.

Gillis, D. J., et W. B. Kemp. 1983. L'exploitation piscicole de la Koksoak, 1977–1981. Sommaire des résultats. Document préparé pour le Groupe d'étude conjoint Caniapiscau–Koksoak par le service de la Recherche, Société Makivik, Montréal. 40 p.

Harlett, A. 1919. Fishes and invertebrates collected by Rev. W. G. Walton in Hudson and James Bay. Ann. Rep. Fish. Can. 1919: 56–67.

Hunter, J. G. 1968. Fishes and fisheries. *In* Science, history and Hudson Bay. Department of Energy, Mines and Resources, Ottawa, Vol. 1: 360–378.

Hunter, J. G., B. T. Kidd, R. Greendale, R. Baxter, and R. Morin. 1976. Fisheries resources of the lower reaches and coastal regions of Eastmain, La Grande, Roggan and Great Whale Rivers from 1973 to 1975, p. 299–322. *In* Environnement-Baie James, symposium 1976, sous l'égide d'Environnement Canada, de la Société de développement de la Baie James et de la Société d'énergie de la Baie James. Montréal.

Huntsman, A. G. 1931. Biological and oceanographic conditions in Hudson Bay. 1. Hudson Bay and the determination of fisheries. Contr. Can. Biol. N.S. 6(7): 455–462.

Hydro-Quebec, et SEBJ. 1985. Suréquipement de l'aménagement de La Grande 2. Rapport sur les études d'avant-projet. 3: Répercussions sur l'environnement. Hydro-Québec et Société d'énergie de la Baie James, Montréal. 506 p.

Jessop, R. L., J. Lee, and, G. Power. 1970. Observations on the fish fauna of the Leaf River, Ungava. Can. Field-Nat. 84: 365–367.

Lalumiere, R., R. Le Jeune, et A. Boudreault. 1985. Répercussions d'une réduction de débit sur les rivières Caniapiscau et Koksoak. Rapport présenté au Groupe d'étude conjoint Caniapiscau–Koksoak par Gilles Shooner Inc., Loretteville, Québec. 117 p.

Laramée, P. 1983. Étude de l'ichtyofaune en aval de la future centrale de LG 1. Analyse des données 1981–1982. Rapport préparé par Eco-Recherches Inc. pour la direction Environnement de la Société d'énergie de la Baie James, Montréal, Québec. 81 p.

Legendre, V. 1962a. Lac Assinica, district de l'Abitibi: expédition en vue d'obtenir des œufs de gros ombles de fontaine (*Salvelinus fontinalis*). Ministère Chasse et Pêcheries, Québec. 20 p.

1962b. Pêche à l'esturgeon, lac Kenonisca. Rapport d'expédition. 8 p. manuscrites.

Legendre, V., et J. Rousseau. 1949. La distribution de quelques-uns de nos poissons dans le Québec arctique. Annales de l'ACFAS, 15: 133–135.

Le Jeune, R. 1964a. Inventaire ichtyologique du lac Mistassini. Qué. Ministère Tourisme, Chasse et Pêche, Serv. Faune, Rap. 3: 349–422.

1964b. Inventaire ichtyologique du lac Assinica. Qué. Ministère Tourisme, Chasse et Pêche, Serv. Faune, Rap. 3: 257–261.

1965. Répertoire préliminaire des poissons du Nottaway. Naturaliste can. 92 (2): 69–75.

1967. L'omble chevalier anadrome du Kagnersoualoudjouark, Service de la Faune du Québec. Bulletin 10: 45 p.

Le Jeune, R., et J. Faucher. 1972. Liste préliminaire des poissoins d'eaux douces de la Radissonie orientale. Naturaliste can. 99: 359–365.

Lindsey, C. C., and, C. S. Woods. 1970. Biology of coregonid fishes. Presented at the International Symposium on biology of coregonid fishes. University of Manitoba Press, Winnipeg, Man. 560 p.

Lower, A. R. M. 1915. A report on the fish and fisheries of the west coast of James Bay. Ann. Rep. Dep. Naval Serv. 1914: 29–67.

Magnin, E. 1964. Premier inventaire de la faune ichtyologique du lac et de la rivière Waswanipi, dans le centre ouest de la province de Québec. Naturaliste can. 91: 273–308.

1965. Croissance de l'esturgeon *Acipenser fulvescens* Raf. vivant dans le bassin hydrographique de la rivière Nottaway, tributaire de la baie James. Naturaliste can. 92: 193–204.

1966. Quelques données biologiques sur la reproduction des esturgeons *Acipenser fulvescens* de la rivière Nottaway. Can. J. Zool. 44: 257–263.

1977. Écologie des eaux douces du territoire de la Baie James. Société d'énergie de la Baie James, Montréal. 454 p.

Magnin, E. et V. Legendre. 1964. Extension d'aire de trois poissons d'eau douce dans le nord-ouest de la province. Québec, Ministère du Tourisme, de la Chasse et de la Pêche, Service de la Faune, Rap. 3: 17–19.

McAllister, D. E., and S. Bleakney. 1958. Some Freshwater fishes from Northeastern Quebec and Labrador. National Museum of Canada, Bull. 166: 31–39.

Melvill, C. D. 1915. Report on the east-coastal fisheries of James Bay. Rep. Fish. Invest. in Hudson and James Bays and tributary waters in 1914. Dep. Nava. Serv. Ottawa. 39^{e}: 7–28.

Messier, D., D. Roy, et R. Lemire. 1985. Évolution du mercure dans les chairs des poissons. *In* Réseau de surveillance écologique du Complexe La Grande 1978–84. Direction Ingénierie et Environnement, Société d'énergie de la Baie James. Montréal. 170 p.

Messier, D., R. G. Ingram, and D. Roy. 1986. Physical and biological modifications in response to La Grande hydroelectric Complex, p. 403–424. *In* I. P. Martini [ed.] Canadian Inland Seas. Elsevier Science Publishers. Amsterdam.

Ministère de l'Environnement du Québec. 1983. Annuaire hydrologique 1981–1982. Direction générale des inventaires et de la recherche, Québec. Ministère de l'Environnement, Québec. 200 p.

MLCP et SAGE. 1980a. Étude des populations de saumons du fleuve Koksoak. 1: Caractéristiques biologiques et évaluation des effectifs. Rapport présenté au Groupe d'étude conjoint Caniapiscau–Koksoak par le Ministère du Loisir, de la Chasse et de la Pêche et la Société d'aménagement général de l'environnement Ltée, Québec. 84 p.

1980b. Étude des populations de saumons du fleuve Koksoak. 2: Effets possibles de la réduction de débit de la rivière Caniapiscau sur les populations de saumons. Rapport présenté au Groupe d'étude conjoint Caniapiscau–Koksoak par le Ministère du Loisir, de la Chasse et de la Pêche et la Société d'aménagement général de l'environnement Ltée, Québec. 22 p.

1981. Étude des populations de saumons du fleuve Koksoak. 3: Essai sur la capacité de production et de récolte potentielles. Rapport présenté au Groupe d'étude conjoint Caniapiscau–Koksoak par le Ministère du Loisir, de la Chasse et de la Pêche et la Société d'aménagement général de l'environnement Ltée, Québec. 43 p.

MLCP, SAGE, et Gilles Shooner Inc. 1982. Biologie du saumon dans les eaux du fleuve Koksoak, en Ungava. Rapport présenté à Hydro-Québec par le Ministère du Loisir, de la Chasse et de la Pêche, la Société d'aménagement général de l'environnement Ltée et Gilles Shooner Inc., Québec. 142 p.

Morin, R., J. J. Dodson, and G. Power. 1982. Life history variations of anadromous cisco (*Coregonus artedii*), lake whitefish (*C. clupeaformis*) and round whitefish (*Prosopium cylindraceum*) populations of eastern James–Hudson Bay. Can. J. Fish. Aquat. Sci. 39: 958–967.

Native Harvesting Research Committee,. 1982. Research to establish present levels of harvesting by native peoples of Northern Québec. Part 1. A report on the harvests by the James Bay Cree, Montréal.

(In preparation). Research to establish present levels of harvesting by native peoples of Northern Quebec. Part 2. Harvests by the Inuit of Northern Quebec, Montreal.

Northcote, T. G., and P. A. Larkin. 1989. The Fraser: a major salmonine production system, p. 172–204. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Power, G. 1966. Observations on the speckled trout (*Salvelinus fontinalis*) in Ungava. Naturaliste can. 93: 187–198.

1969. The Salmon of Ungava Bay. Arctic Institute of North America. Technical paper no 22. 72 p.

Power, G., et D. R. Oliver. 1961. Notes on the distribution and relative abundance of fresh water fish in Ungava. Canadian Field-Nat. 75: 221–224.

Prinsenberg, S. J. 1977. Freshwater budget of Hudson Bay. Manuscript report series no 5. Ocean and aquatic sciences, Canada center for inland waters, Burlington, Ontario, Canada. Unpublished manuscript. 71 p.

Radforth, I. 1944: Some considerations of the distribution of fishes in Ontario. Contr. Roy. Ont. Mus. Zool. 25: 116 p.

Randall, R. G., M. F. O'Connell, and E. M. P. Chadwick. 1989. Fish production in two large Atlantic Coast rivers: Miramichi and Exploits, p. 292–308. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Richardson, L. R. 1944. Brief record of fishes from Central Northern Quebec. Copeia 1944: 205–208.

Roy, D. 1985. Zooplancton. *In* Réseau de surveillance écologique du Complexe La Grande. Direction Ingénierie et Environnement, Société d'énergie de la Baie James, Montréal. 92 p.

Ryder, R., W. B. Scott, and E. J. Crossman. 1964. Fishes of Northern Ontario, north of the Albany River. Contr. Roy. Ont. Mus. Zool. 60: 30 p.

SAGE. 1981. Étude limnobiotique du bassin inférieur de la rivière Caniapiscau. Rapport présenté à la Société d'énergie de la Baie James par la Société d'aménagement général de l'environnement Ltée, Québec. 70 p. et appendices.

Schlesinger, D. A., and H. A. Regier. 1982. Climatic and morphoedaphic indices of fish yield from natural lakes. Tran. Amer. Fish. Soc. 111: 141–150.

Schetagne, R., et D. Roy. 1985. Physico-chimie et pigments chlorophylliens. *In* Réseau de surveillance écologique du Complexe La Grande. Direction Ingénierie et Environnement, Société d'énergie de la Baie James, Montréal. 142 p.

SDBJ, et Environnement Canada. 1980. Étude sur l'Environnement. Territoire de la Baie James. Rapport synthèse 1972–1979. Société de développement de la Baie James et Environnement Canada, Montréal. 303 p.

SEBJ (SOCIÉTÉ D'ÉNERGIE DE LA BAIE JAMES). 1978. Connaissance du milieu des territoires de la Baie James et du Nouveau-Québec. Société d'énergie de la Baie James, Montréal. 297 p.

SEBJ ET SOTRAC. 1985. Étude des effets du détournement des rivières Eastmain et Opinaca en aval des ouvrages de dérivation. Synthèse des résultats du suivi environnemental de 1980 à 1984. Société d'énergie de la Baie James et Société des travaux de correction du Complexe La Grande, Montréal. 256 p.

SEDELL, J. D., J. E. RICHEY, AND F. J. SWANSON. 1989. The river continuum concept: a basis for the expected ecosystem behavior of very large rivers? p. 49-55. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

TSEEB, Y. Y. 1962. On certain regular features associated with the formation of the hydrobiological regime in the Kokhovsk Reservoir. (Transl. from Tr. Zon. Sov. po Tipol i Biol. Obzn. Rib. Ispol. Vnut. Youzh. Zony SSSR, p. 204–210.)

VANNOTE, R., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND, C. E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

VLADYKOV, V. D. 1933. Biological and oceanographic conditions in Hudson Bay. 9. Fishes the Hudson Bay Region (except the Coregonidae). Contr. Can. Biol. N.S. 8: 16–61.

WEINSTEIN, M. D. 1976. What the land provides. An examination of the Fort George subsistence economy and the possible consequences on it of the James Bay hydroelectric project. Report of the Fort George Resource Use Study. Grand Council of the Crees (of Qué.), Montréal. 255 p.

The Fraser River: A Major Salmonine Production System

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Abstract

NORTHCOTE, T.G., AND P.A. LARKIN. 1989. The Fraser River: A major salmonine production system, p. 172–204. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Historically the Fraser was the greatest producer of salmonine fishes of any single large river in the world and currently retains that position with an average annual abundance of nearly 14 million Pacific salmon (*Oncorhynchus*) and an overall yield (commercial and recreational) exceeding 12 million salmonines annually. Causes for high production are examined in the Fraser's geological, morphometric and hydrological features, water quality and nutrient supply, salmonine diversity and juvenile rearing capacity, and fisheries management practices. Most of the ten major sub-basins drain sedimentary and volcanic formations providing good water quality and moderate nutrient supply from sparsely populated areas. Low mainstem gradient for 1 200 km inland from its mouth permits undammed access to upstream migrating salmonine fishes into many high quality spawning streams and juvenile rearing habitats. Parts of the lower mainstem river also provide spawning areas for several million salmon. Genetically distinct salmonine stocks exploit sub-basin and local drainage diversity in maximizing reproductive success. Portions of several sub-basins, the lower mainstem and estuary have been negatively affected by other resource uses. Heavy commercial and recreational fishing pressure occurs on most species and stocks. Nevertheless for many, numbers have not declined dramatically from historic levels. With continued management and enhancement most salmonine populations probably can be restored to at least historic levels.

Résumé

NORTHCOTE, T.G., AND P.A. LARKIN. 1989. The Fraser River: a major salmonine production system, p. 172–204. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Au niveau historique, le fleuve Fraser était le plus grand producteur de salmonidés parmi tous les grands cours d'eau du globe; il en va toujours de même: l'abondance annuelle moyenne se situe à environ 14 millions de saumons du Pacifique (*Oncorhynchus*) et un rendement global annuel (pêches commerciale et sportive) qui dépasse 12 millions de salmonidés. Les facteurs à la base de cette production élevée sont étudiés à la lumière des caractéristiques géologiques, morphométriques et hydrologiques du Fraser, de la qualité de l'eau, de l'apport en bioéléments, de la diversité des salmonidés et de la capacité de croissance des juvéniles ainsi que des méthodes de gestion des pêches. La plupart des dix principaux bassins secondaires drainent des formations sédimentaires et volcaniques, générant ainsi une bonne qualité de l'eau et un apport modéré de bioéléments provenant de régions peu peuplées. Le faible gradient du tronçon principal s'étendant sur 1 200 km de l'embouchure vers l'intérieur des terres constitue une voie d'accès libre aux salmonidés en migration vers l'amont de nombreux cours d'eau qui serviront de zones de ponte et d'aires de croissance des juvéniles de qualité élevée. Certaines parties du tronçon inférieur servent aussi de frayère à plusieurs millions de saumons. Afin de maximiser le succès de la reproduction, des stocks de salmonidés génétiquement différents exploitent la diversité des bassins secondaires et des aires de drainage local. Certaines parties de plusieurs bassins secondaires, la partie inférieure du tronçon principal ainsi que l'estuaire ont été négativement touchés par l'exploitation d'autres ressources. La plupart des espèces et des stocks font l'objet d'une pression par pêche commerciale et sportive élevée. Malgré cela, l'abondance n'a pas sérieusement changé par rapport au niveau historique. Le rétablissement de la plupart des populations de salmonidés, au moins à leur niveau historique, nécessitera une gestion et une mise en valeur soutenues.

Introduction

The Fraser has long been said to be one of the great salmon rivers of the world. Indeed, to those who grew up along its shores or to those who have written so sensitively of its salmon bounty (Hutchinson 1950; Lyons 1969; MacLennan 1974), this claim hardly seems worthy of question. But those who recently have attempted to document its overall salmonid production (Northcote 1974, 1976; Argue et al. 1986; Birtwell et al. 1986) did not try to position its status in relation to other rivers of the Pacific northwest or to those throughout the native and introduced salmonid distribution of the world. This we took as a major objective, not to "prove the obvious" but rather to see if we could clarify why it should be so, once its position was confirmed.

To meet general objectives of the LARS symposium we have summarized information on morphometry, hydrology, and other characteristics affecting production which are useful in rationalizing the high salmonine output of the system. After a brief review of some of the more important aspects of the geology and geography of the watershed, we then consider river water quality as well as primary and secondary producers, before turning to note the past and present fish fauna. Then we focus specifically on salmonine diversity and relative abundance in the Fraser in relation to other large river producers of salmonine fishes throughout the world. Following a summary of salmonine management practices, effects of dams and diversions, importance of waterfowl, wildlife and recreational values, we conclude with an assessment of major factors responsible for the high salmonine productivity of the Fraser system. We follow the classification of Nelson (1984) who recognizes under the family Salmonidae the subfamily Salmoninae which includes, in large rivers, five genera — *Brachymystax, Hucho, Salvelinus, Salmo,* and *Oncorhynchus.*

Origin, Glaciation, Discovery, and Development

The Fraser, as well as several other large rivers entering the North Pacific coast (Columbia, Skeena, Nass, Stikine), flows in a westerly direction through deeply cut valleys across a region of Miocene uplift. It is thought to have existed in essentially that course since the Pliocene, some 12 million years ago (McPhail and Lindsey 1986). Along much of its middle canyon north of Hope, the Fraser follows a steeply dipping fault between the hard granitic intrusives of the coastal mountains and the stratified softer interior rocks (Fig. 1) which underlie most of the drainage basin. This canyon may have been formed as early as the Miocene, some 20 million years ago (Robinson 1985).

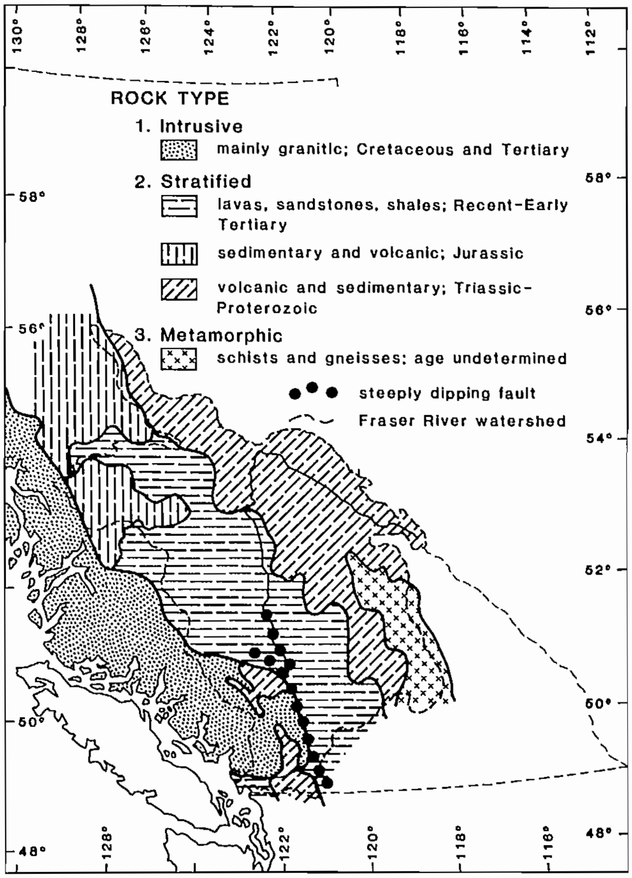


FIG. 1. Generalized geology of the Fraser River watershed. Adapted from Farley (1979).

Several Pleistocene glaciations covered at some time the entire Fraser drainage basin though there were intervening ice-free periods in many areas. The upper ice-surface contour was at least 2400 m over most of the middle and upper basin and only dropped near the present coastline to surfaces of about 1000 m (Farley 1979). Following the penultimate glacial period much of the lower Fraser basin remained free of ice until about 19 000 years ago (Clague et al. 1980). The subsequent and final relatively rapid build-up of ice did not occur near the present Fraser mouth until after 18 000 B.P., and the area was once again ice-free by about 13 000 B.P. Between 13 000 and 11 000 B.P. the Fraser Lowland underwent a complex series of changes in relative sea level (Armstrong 1981).

Deglaciation of the last (Fraser) glacial ice mass was mainly by down-wasting which first freed the uplands but left ice tongues in pre-existing valleys. Such stagnant tongues as well as active ice lobes ponded a complex series of large glacial lakes (Fulton 1969; Tipper 1971) mainly in the Fraser uplands (Fig. 2). Many of these lakes were marked by several level changes with connections to other major (non-Fraser) systems. For example, the earliest glacial lake in the present Nicola basin drained south to the Columbia River but two subsequent lower stage lakes connected to the north with another glacial lake complex draining east and eventually south into Okanagan–Columbia drainages. Several very large glacial lakes formed in the north central portion of the Fraser basin and drained north easterly into the Peace–Mackenzie system which about 1 500 years earlier had Mississippi connections (Lindsey and McPhail 1986). In the southern interior at least, all glacial lakes were drained and the modern drainage was established prior to 8 900 years B.P. (Fulton 1969).

Between 9 000 and 10 000 years B.P. the formation of the Fraser delta commenced (Armstrong 1981). About 8 000 years ago the delta began to fan out and built up 100–200 m thick deposits over Pleistocene sediments (Mathews and Shepard 1962). Although the form and extent of the Fraser delta and marsh areas have changed greatly over the last 150 years (Kistritz 1978), the shore has been close to its present level for the last 5 500 years (Mathews et al. 1970).

The geography of the Fraser was no doubt known, at least in parts, by the various indigenous native tribes who used the river in their trading expeditions. The fur trader and explorer Alexander Mackenzie entered the Fraser in 1793 from the headwaters of the Parsnip River (Peace drainage), thinking he had reached the Columbia drainage. Proceeding downstream below the confluence of the Quesnel and the Fraser, Mackenzie learned from the natives that the river ran south and became impassable, so he turned back upstream to the West Road River from whence his party marched overland to the Pacific (Ormsby 1958). Simon Fraser explored much of the northeast part of the river in the period 1804-1807 and in 1808 made the hazardous journey through the canyon to Hope, subsequently reaching tide water to realize that the river could not be the Columbia for its mouth was 3° of latitude too far north (Ormsby 1958).

British Columbia now has a population of over 2.5 million, of which about 80% live in the Fraser River water-

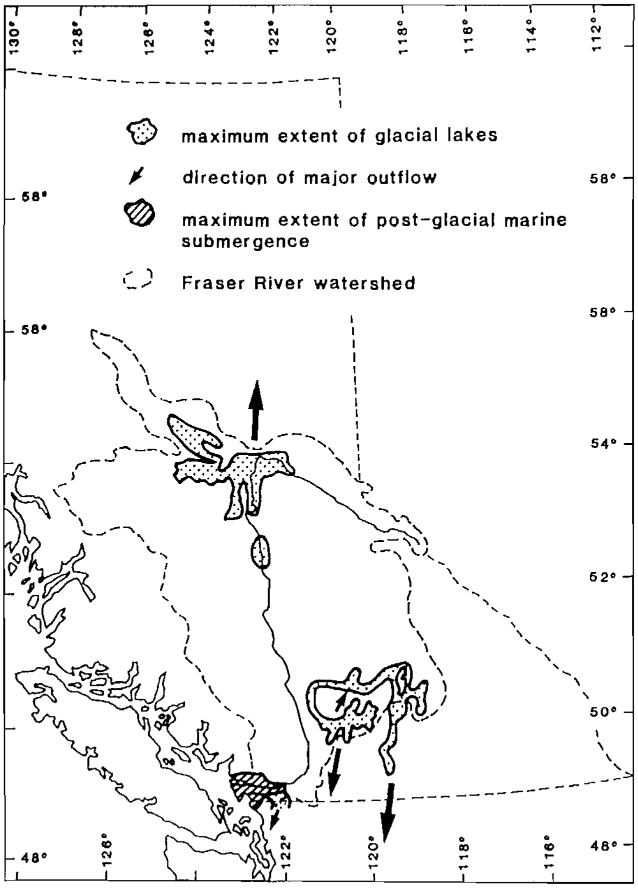
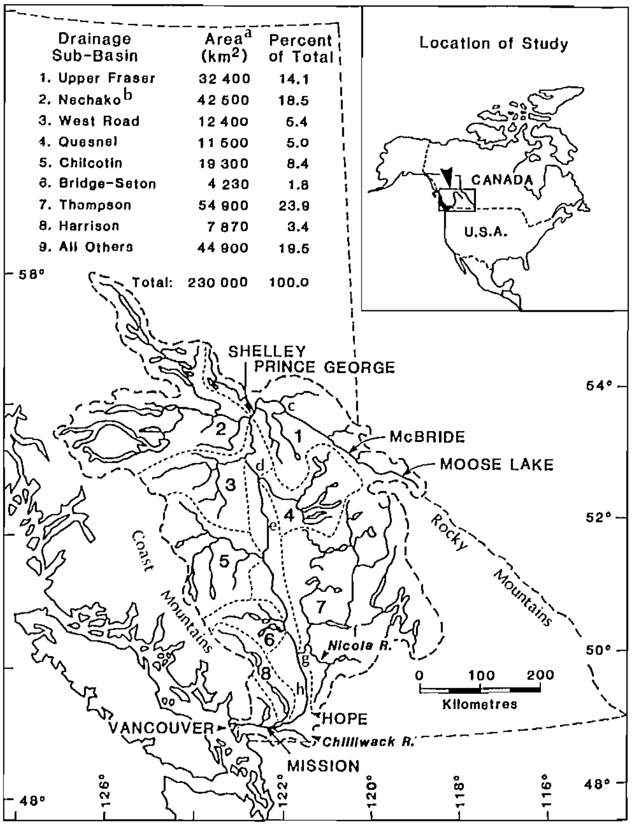


FIG. 2. Location and outflow direction of major glacial lakes associated with late deglaciation stages of the Fraser River watershed. Adapted from Farley (1979).



Drainage Sub-Basin	Area[a] (km²)	Percent of Total
1. Upper Fraser	32 400	14.1
2. Nechako[b]	42 600	18.5
3. West Road	12 400	5.4
4. Quesnel	11 600	5.0
5. Chilcotin	19 300	8.4
6. Bridge-Seton	4 230	1.8
7. Thompson	54 900	23.9
8. Harrison	7 870	3.4
9. All Others	44 900	19.5
Total:	230 000	100.0

FIG. 3. Major drainage sub-basins of the Fraser River watershed. [a]does not include a small portion for some tributaries between recording station and confluence with the Fraser River, [b]includes 14 000 km² behind Kenney Dam, [c]Hansard, [d]Quesnel, [e]Williams Lake, [f]Kamloops, [g]Lytton, [h]Hell's Gate, [i]New Westminster. Inset shows Fraser River in North America.

shed. Within the watershed 86 % of the people are concentrated in the lower Fraser Valley below Hope, and most of the remainder are divided about equally between the Thompson River sub-basin (Fig. 3 — mainly in and around the few urban centres) and the mainstem middle reaches from Hope to Prince George. Most other sub-basins have very low and dispersed populations, the largest (slightly over 20 000) being in the Nechako sub-basin.

The major urban-industrial area of the province is situated around Vancouver, much of it astride the Fraser's lower reaches and estuarine North Arm (Dorcey 1976, 1986). Inland, the lower Fraser Valley is dominated by agriculture (mainly, dairy, poultry, fruit and vegetable farms dairy), and cattle ranching is predominant throughout the central and northern sub-basins (Farley 1979). Well over half of the Fraser watershed is forested and supports active logging, the major exceptions being the agricultural lands of the lower Fraser Valley, the open interior grasslands of the Thompson, Chilcotin and middle Fraser canyon, and the higher elevations of the coastal and interior mountain ranges. Large sawmills are clustered in the lower Fraser Valley, in the Thompson sub-basin, along the mainstem Fraser canyon and in the Nechako sub-basin. Three moderate sized pulp mills are located at Prince George, two at Quesnel and another near Kamloops in the Thompson sub-basin. Although the Fraser River gold rush in the mid 19th century played a major role in development of the province, most mining now is focussed on base metals in the interior sub-basins (several major concentrators in the Thompson sub-basin, one in the middle canyon and one in the Nechako sub-basin) and structural materials (sand, gravel) in the lower Fraser Valley. A few small generating stations on tributaries of the lower Fraser and the Bridge–Seton sub-basin (Fig. 3) represent the only significant hydro-electric development on the Fraser, apart from the major diversion of the Nechako sub-basin headwaters to a mid-coast station. Since the gold rush, transportation routes have followed the Fraser River and its tributaries into the interior and today three major railways run for substantial distances along its mainstem or tributary banks as do a number of main highways. In addition, the largest airport of the province has been developed on an island in the Fraser estuary. Finally, a major part of provincial outdoor recreation and tourism occurs within the Fraser watershed (Farley 1979).

Morphometry and Hydrology

The mainstem Fraser sweeps in a gigantic S-shaped course (Fig. 3), originating on the western slopes of the Rocky Mountains and terminating in the Pacific Ocean at Vancouver, having drained about one quarter of the total area of British Columbia. Seven major tributaries along with

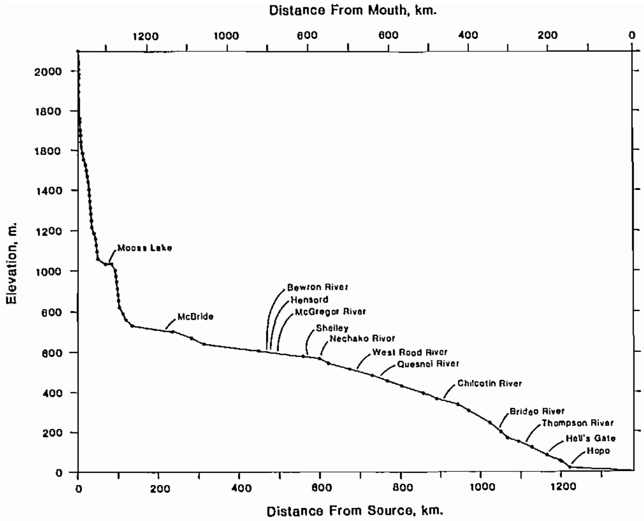


FIG. 4. The longitudinal profile[a] of the Fraser River.
[a]based on 1:50 000 scale National Topographic maps with 30.5 m contour interval.

the upper headwaters of the mainstem river comprise over 80 % of its total drainage basin (Fig. 3) and two of these tributaries alone (Nechako and Thompson) account for over 42 % of the total.

Over most of its 1 375 km length, the Fraser River flows in a well-defined narrow channel and only in a few upper reaches and in its lowermost 150 km does the channel at low flow show obvious braiding. In these lower reaches many of the sloughs, meanders, and other backwaters have been cut off or modified by agricultural dyking, road and railway construction or urban and industrial development. In profile (Fig. 4) the Fraser does not closely follow the theoretical ideal (Welcomme 1985) as this is interrupted near the headwaters by Moose Lake, the only sizeable lake in the mainstem river, as well as by two upriver low slope areas near McBride and Hansard. The Fraser originates at a moderately high elevation (2 100 m), but much of this is lost in the first hundred kilometres so that the river from an elevation of 700 m is almost 1 200 km long (Fig. 4).

Although already a 5th order watershed at the outlet of Moose Lake in its upper reaches, the Fraser here has gathered little more than one percent of its total discharge (Table 1). At Shelley, just upstream from the Nechako, the Fraser has nearly a quarter of its total discharge and with the additions of four other major tributaries (West Road, Quesnel, Chilcotin, and Bridge–Seton) it is still well under half of its total. Of the three largest and unregulated of these tributaries, two lie in the rain shadow of the Coast Mountains and flow east into the Fraser (West Road, Chilcotin) whereas the third and smaller (Quesnel) flows west from an area of much higher precipitation. Thus the mean annual discharge per km^2 of drainage basin for the latter is 0.021 $\mathrm{m}^3 \cdot \mathrm{s}^{-1}$ compared to 0.003 and 0.005 $\mathrm{m}^3 \cdot \mathrm{s}^{-1}$ for the West Road and Chilcotin, respectively. With the entrance of the Thompson River, by far the largest discharge of any tributary (Table 1), the Fraser reaches two-thirds of its total volume. At Hell's Gate (Fig. 4) between Lytton and Hope, the river rushes through nearly vertical rock walls at a surface velocity which may exceed 7.5 $\mathrm{m} \cdot \mathrm{s}^{-1}$ and where the minimum and maximum water level may differ as much as 32 m. Although the Harrison River drains the smallest subbasin of any of the major tributaries (just over 3 percent; Fig. 3), its 451 $\mathrm{m}^3 \cdot \mathrm{s}^{-1}$ flow is the second highest and its discharge per unit drainage area (0.057 $\mathrm{m}^3 \cdot \mathrm{s}^{-1} \cdot \mathrm{km}^{-2}$) the highest — no doubt largely a result of its location in the Coastal Mountains with very high rainfall. During freshet the Fraser River frequently discharges over 12 000 $\mathrm{m}^3 \cdot \mathrm{s}^{-1}$. Minimum daily flows for most of the major tributaries as well as the mainstem Fraser usually occur in winter (December–February) although in a few tributaries they extend into early spring (Table 1). Maximum daily flows are usually in late spring to early summer, reflecting the controlling influence of snow and glacial meltwater. Because of the more continental climate of much of the watershed and the balancing effect of large lakes, most sizeable Fraser tributaries do not exhibit the 100 to 1 000-fold change between minimum and maximum flow so characteristic of British Columbia rivers whose watersheds are entirely coastal.

TABLE 1. Discharge ($\mathrm{m}^3 \bullet \mathrm{s}^{-1}$) characteristics for the mainstem Fraser River and its major tributaries at the station closest to their confluence.[a]

River	Order (Approx.)	Mean annual	Cumulative % mean annual	Minimum daily (date)	Maximum daily (date)
Fraser (Red Pass)	5	47	1.3	4 (Mar. 30)	402 (June 12)
Fraser (McBride)	5	198	5.5	19 (Dec. 28)	1390 (June 12)
Fraser (Shelley)	6	819	22.8	92 (Feb. 18)	4980 (June 14)
Nechako[b]	6	300	31.1	41 (Apr. 15)	1080 (July 7)
West Road	6	35	32.1	7 (Jan. 30)	377 (May 9)
Quesnel	6	236	38.6	28 (Mar. 20)	1160 (June 13)
Chilcotin	6	98	41.3	14 (Jan. 13)	493 (Aug. 10)
Bridge–Seton[b]	5	115	44.5	9 (Mar. 30)	658 (May 31)
Thompson	7	786	66.4	125 (Jan. 17)	4130 (June 15)
Harrison	4	451	78.9	66 (Feb. 27)	1930 (June 24)
Fraser (Mission)	8	3410	94.7	648 (Feb. 15)	14400 (June 17)
Fraser (mouth)	8	3600	100.0		

[a] Data from Water Survey of Canada, Historical Streamflow Summary, British Columbia 1984, Ottawa, Canada 1985; most data represent averages for 25 or more years of records.
[b] Regulated.

Tidal influence extends about 100 km up the Fraser River from its mouth and one sizeable tributary, the Pitt River (mean annual flow > 60 m^3 • s^{-1}), over 30 km upstream, undergoes regular reversals of flow during incoming tides. At the mouth, the mean tidal range is about 3 m and about 1 m at New Westminster, 30 km upstream. During freshet, tidal influence is greatly reduced and only detectable near the mouth where average velocities of nearly 3 m • s^{-1} occur, though for much of the year flows of 1.5 to 2 m • s^{-1} are common in main channels of the lower reaches. Consequently, marshes and tidal channels within the Fraser estuary are not strongly influenced by saltwater intrusion.

As the lower valley was settled and developed for agriculture in the latter part of the 19th century it became increasingly apparent that dykes were necessary to prevent flooding either from the spring freshet or the occasional winter combination of heavy rain and high tide. After a flood in 1948 there was an intensive program of extending and strengthening dykes. Today, the river is extensively dyked in the lower reaches, with pumping of small tributaries into the main stem when it is at high water levels. The largest land reclamation involved diversion of the Chilliwack River into a canal, coupled with the dyking of the Sumas River and subsequent draining in 1924 of over 12 000 ha of marshland nearly 1 m below mean sea level, known as Sumas Lake.

Water Quality and Nutrients

Suspended Sediment

The Fraser River is usually characterized as a silt-laden system, but one with marked seasonal changes (Table 2) approximately in response to discharge. The minimum recorded daily concentration of suspended sediment (1 mg • L^{-1}), which usually occurs in December or January, does not change between Hansard in its upper reaches and Hope at the start of its lower reaches. Nor is there much regional change in maximum daily concentration over that distance (1650 and 1460 mg • L^{-1} for Hansard and Hope, respectively) with a decrease to 765 mg • L^{-1} in the slower moving waters at New Westminster. Most of the suspended sediment transport of the river occurs during late spring to early summer, the months of May and June together accounting for over half of the load in the upper reaches and about two-thirds in the lower reaches (Table 2).

The annual total load of 18.2 million tonnes is close to the 20 to 25 million tonnes said to be deposited by the Fraser annually in the Strait of Georgia (Joy 1975). Compared to some large rivers (Table 2.5, Welcomme 1985), the sediment yield of the Fraser seems paltry.

Highest turbidity values occur between May and August for almost all mainstem stations (Clark et al. 1981) with some middle reach stations having > 100 Jackson Turbidity Units (JTU) and most exceeding 30 JTU except in the uppermost reaches. In winter, turbidity throughout the system usually is < 30 JTU, with readings as low as 2–3 at Hell's Gate. Secchi disc transparency in the mainstem and arms of the lower Fraser River ranged from maxima slightly over 1 m in February–March to minima less than 20 cm in May–June (Northcote et al. 1975a) whereas the depth of 1 % surface illumination dropped from about 3 m down to less than 1 m during the same periods.

Organic Carbon

The total particulate organic carbon (POC) load of the Fraser River has never been adequately estimated. Seasonally, two peak periods might be expected, one in late-spring to summer during freshet (mainly large POC — trees, stumps, branches) and the other in late autumn (mainly deciduous leaves). Estimates for natural wood debris range between 3 149 and 24 092 m^3 (1971–73) to which must be added "unnatural" wood debris coming largely from activities of the forest industry (Fairbairn and Peterson 1975), which in 1972 amounted to 174 078 m^3. At that time, forestry-related additions determined the large POC load. More recently, a wood debris trap has been operated on the Fraser below Hope, and in 1984 it collected about 90 percent of the debris moving down the river during the major freshet period (Anonymous 1985). No estimates of fine POC load seem to be available for the river.

Dissolved organic carbon (DOC) concentrations have been measured at stations in all three major reaches of the river (Table 3). Seasonally, highest values (up to 16 mg • L^{-1}) occur in the summer or autumn with lowest values in winter to early spring. There seems to be little regional change in DOC levels along the system with about the same range in concentration at upper, middle and lower reach stations. The average annual DOC load of the Fraser River at its mouth has been roughly estimated at 450 000 t by Kistritz (1978) who suggests that the autochthonous carbon production in the Fraser estuary would be about an order

TABLE 2. Seasonal changes in the Fraser River suspended sediment load.[a]

Reach (Station)	Years[b]	% Contribution to monthly means (t • d^{-1})						Annual mean t • d^{-1}	Annual total t 10^3
		J–F	M–A	M–J	J–A	S–O	N–D		
Upper (Hansard)	1972 – 1983	0.3	3.9	55.4	30.6	8.7	1.1	5 818	2 307
Mid (Marguerite)	1971 – 1983	0.6	14.8	61.7	16.8	4.9	1.2	27 470	10 013
Lower (New Westminster)	1965 – 1972	1.6	5.6	66.1	20.5	4.0	2.2	49 700	18 200

[a] Data summarized from Environment Canada, Inland Waters Directorate, Water Resources Branch, Canadian Rivers Sediment Data publications.

[b] Data not complete for all years at all stations.

TABLE 3. Seasonal changes in organic carbon concentration (mg • L^{-1}) in the mainstem Fraser River.[a]

Reach (Stations)	Jan.-Feb.	Mar.-Apr.	May-June	Jul.-Aug.	Sept.-Oct.	Nov.-Dec.
Upper						
(McBride,	<1-3.5	1-9	1-8	<1-15.3	1-9	<1-4
Hansard)	(5)	(6)	(36)	(48)	(2)	(19)
(Shelley)	5-6	<1	5-12	1-16	<1-10	3-8
	(1)	(1)	(8)	(15)	(6)	(7)
Mid						
(Red Rock,	6-9		4-15	2-7	6-11	4-11
Quesnel)	(4)		(10)	(15)	(4)	(9)
(Marguerite -	1-10	<1-7	2-16	1-7	<1-6	<1-7
Hope)	(6)	(3)	(10)	(12)	(4)	(7)
Lower						
(Mission)	<1	1-7	3-5	3-6	<1-5	1
	(1)	(3)	(3)	(2)	(2)	(1)
(New Westminster)	1-4.9	2-6.4	5-8.7	2-3	2-7	<1-3
(Arms)	1-5.0	1-9.8	4-9.6	<1-6	1-16	<1-4
	(>10)	(>19)	(>10)	(12)	(>18)	(12)

[a] Data summarized from Environment Canada, Inland Waters Directorate, Water Quality Branch, British Columbia Water Quality Data 1961-71; Benedict et al. 1973; Hall et al. 1974; Clark et al. 1981; sample sizes in parentheses.

of magnitude lower, i.e. 45 000 t, and that the load supplied by the river would be much greater than that provided to its estuary by Strait of Georgia tidal waters.

Dissolved inorganic carbon levels in the mainstem Fraser ranged from about 10-30 mg • L^{-1} which seemed typical of British Columbia rivers (Clark et al. 1981).

Conductivity

A complex hysteresis has been demonstrated for the conductivity-discharge relationship of the mainstem Fraser River at low order as well as high order stations (Whitfield and Schreier 1981). Nevertheless, an overriding seasonal pattern with higher conductivity during low flow winter months and lower conductivity during high flow summer months seems evident at most upper, middle and lower reach stations on the river (Fig. 5). The magnitude of seasonal change in conductivity for the mainstem river is greatest at the upper reaches where, in winter, conductivities range as high as 220 μS • cm^{-1} and as low as 80 μS • cm^{-1} or less in summer, probably reflecting low flow drainage off soluble limestone formations of the Rocky Mountains and high flow mainly from snow and ice melt. At middle reach stations (Quesnel, Hope) the magnitude of seasonal change is progressively dampened and the conductivity level is lowered so that values rarely exceed 180 μS • cm^{-1} at Quesnel or 150 μS • cm^{-1} at Hope. This trend is continued at Mission and New Westminster (Fig. 5), although there seems to be a double rise and fall over the seasons with highest conductivity in late winter-early spring and again in early autumn, with lowest values in mid-summer, but intermediate levels in mid winter, possibly arising from heavy low-level coastal rainfall. In the delta arms of the river, conductivity increases greatly because of sea water intrusion during low discharge periods (August-May) but during the June-July freshet values are close to those in the lower mainstem (Fig. 5).

Major Ions

A detailed discussion of chemical characteristics of water quality in the upper Fraser River basin is given by Whitfield (1983) who recognizes three reaches where water quality properties are relatively consistent. Sharp changes in geometric mean concentrations of major ions as well as nutrients occur between the reaches, also evident in several cases for the arithmetic means (Fig. 6) which usually are only slightly greater than the geometric means.

Two of the major ions, calcium and bicarbonate, reach highest concentrations in the middle reaches of the river (Fig. 6), although calcium, like several other ions, increases sharply again in the estuary. Magnesium remains relatively constant from the headwaters to Lytton and then gradually decreases in the lower reaches of the river. Sulphate also is relatively constant in the upper reaches down to Dome Creek but then decreases to a mean of about 7.5 mg • L^{-1} maintained from about Prince George to Hope. Potassium is lowest in concentration in the headwaters, increases sharply at Dunster and then after a slight decline at Prince George increases again to reach maximal concentration in the lower canyon to Hope. The mean concentration of sodium and chloride track each other closely, being very low in the headwaters and downstream to Prince George, where they increase rapidly, reaching near maximal levels at Quesnel which are maintained down to the estuary. Whitfield (1983) suggests that as the Fraser River mainstem remains largely within quarternary sediment deposits, the changes in ionic concentration along its length must mainly be due to tributary influence.

Nutrients, pH, Temperature, and Dissolved Oxygen

Mean concentrations of three primary nutrients are lowest in the upper headwaters of the Fraser River (Fig. 7), gradually increase downstream and reach highest levels in mid-canyon stations. Nitrite plus nitrate and total phosphorus

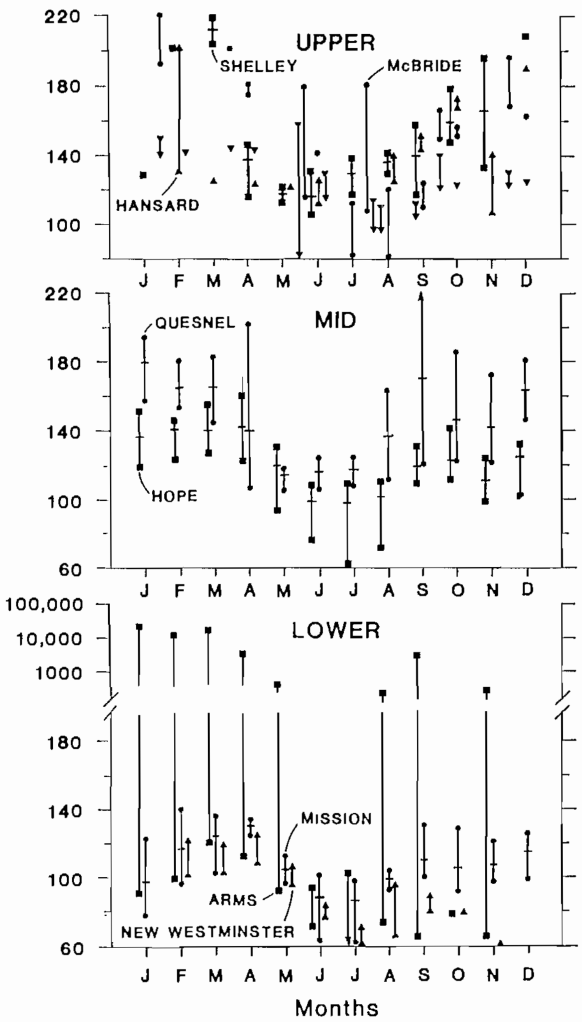


FIG. 5. Seasonal changes in water conductivity range for different reaches and stations on the Fraser River mainstem. Data mainly for 1961–71 (Anonymous 1974) supplemented for upper reaches by 1975–76 monthly data from P.H. Whitfield, Canada Inland Waters Directorate (as well as 1975–76 bimonthly data of Clark et al. (1981) for the same years shown between months) and for lower reaches (Arms) by data in Benedict et al. (1973) and Hall et al. (1974); short horizontal bars on range lines show, where possible, arithmetic means.

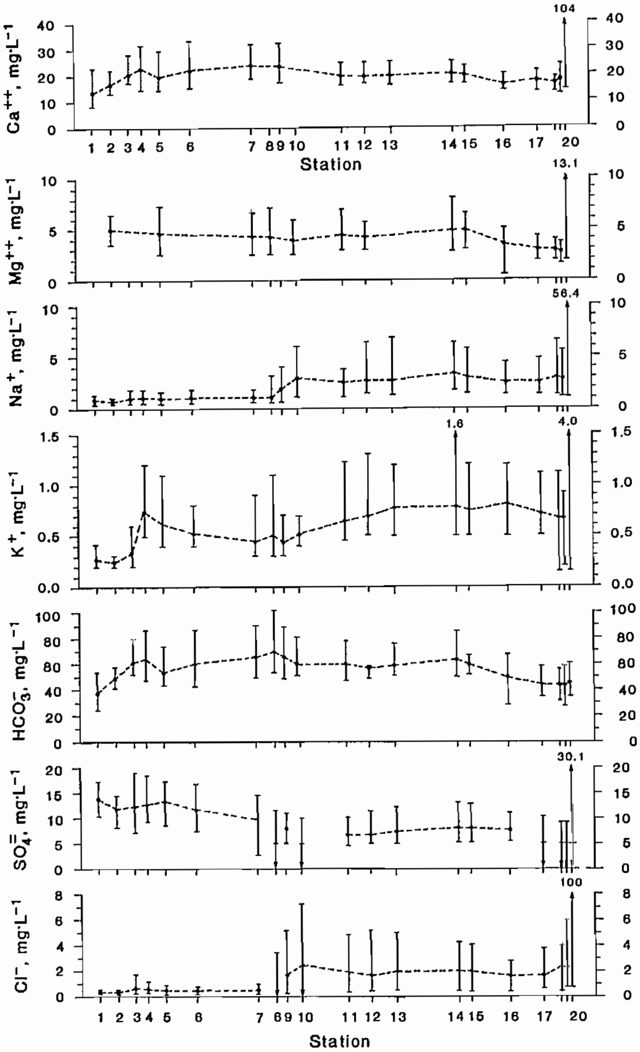


FIG. 6. Concentration of major cations and anions (1975–76) along the mainstem Fraser River from its headwaters to its estuary. Vertical lines with bars give ranges and arithmetic means (shown where appropriate). Data mainly from P.H. Whitfield, Canada Inland Waters Directorate, Vancouver B.C., supplemented for stations 8, 10, 17–20 from Clark et al. (1981) except for Ca^{++} stations 17–20 (1973) from Hall et al. (1974). Station 1 = Yellowhead, 2 = Red Pass, 3 = Tete Jaune Cache, 4 = Dunster, 5 = McBride, 6 = Dome Creek, 7 = Hansard, 8 = Shelley, 9 = Prince George (I. Pulp), 10 = Red Rock Canyon, 11 = Quesnel, 12 = Marguerite, 13 = Chilcotin Bridge, 14 = Lillooet, 15 = Lytton, 16 = Hope, 17 = Mission, 18 = New Westminster, 19 = North Arm (Queensborough Bridge), 20 = South Arm (above Deas Island).

decrease again in the lower reaches whereas silicate shows very little decrease. Concentrations of the two combined nitrogen species and of total phosphorus are very low even at maximum levels in the Fraser when compared to more enriched river systems in Europe (Vollenweider 1968), but for nitrogen are not much less than the North American average (Golterman 1975). Silicate concentrations in the lower reaches of the Fraser are similar to the North American river water average (4.2) but below the world river average of 6.6 (Golterman 1975).

After a small increase in pH at the Fraser headwaters (Fig. 7) mean levels remain nearly constant at just under 8 along most of the river course with a slight decrease again in the lower reaches. Little change is evident at stations where averages were available for earlier and more recent sampling periods (Fig. 7).

Except in the lower reaches, minimum water temperature along the length of the mainstem Fraser is close to 0°C. (Fig. 7). Maximum temperatures slightly over 20°C were attained below Prince George in 1975, but no doubt other stations slightly exceed that level on other years as most other downstream stations have maxima close to 20°C. The seasonal pattern of temperature change is similar at upper, mid and lower reach stations with a minimum in January and a maximum in August (Fig. 8).

Minimum dissolved oxygen concentrations are above 8 mg • L^{-1} (Fig. 8) except very occasionally in middle reaches and more often in the slower moving, lower dis-

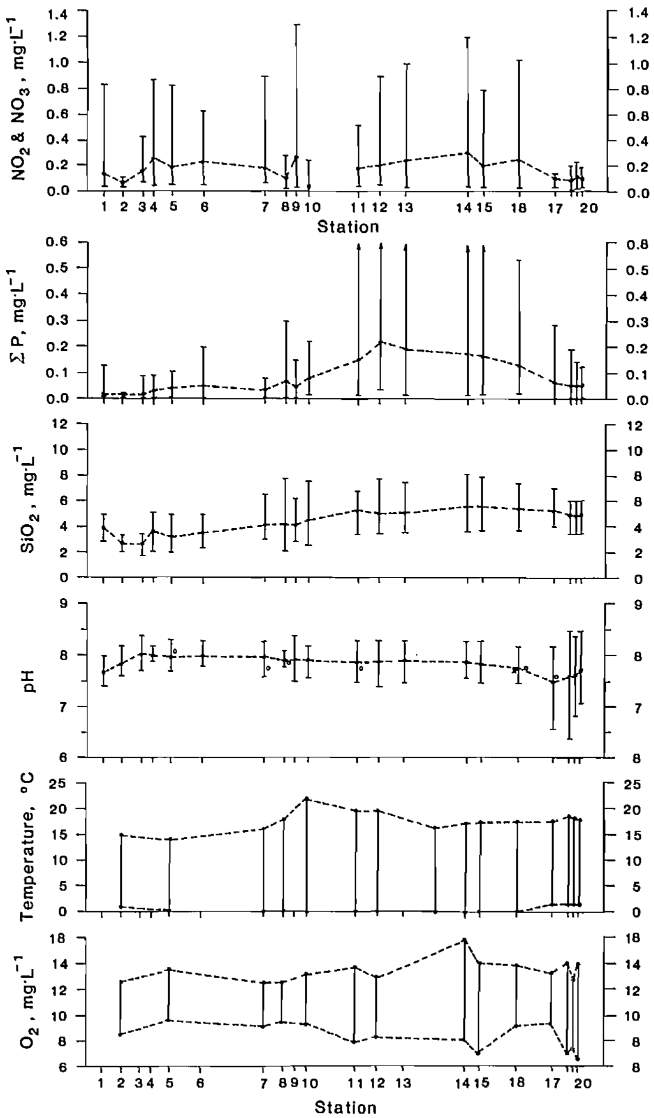


FIG. 7. Concentration of three major nutrients, pH level, water temperature and dissolved oxygen (1975–76) along the mainstem Fraser River from its headwaters to its estuary. Vertical lines with bars give ranges and arithmetic means (shown where appropriate). Data from P.H. Whitfield, Canada Inland Waters Directorate, Vancouver, B.C. and for nutrients and pH at stations 8, 10, 17–20 as well as all temperature and dissolved oxygen values from Clark et al. 1981. Stations as in Fig. 6 except a = Big Bar, o = pH average 1961–71 (Anonymous 1974), x = pH average 1979–81 (Thorp 1985).

charge of the estuarine North Arm where at a few locations values approaching 2 mg • L^{-1} were recorded (Benedict et al. 1973) in the period before diversion and treatment of sewage. Maximum levels are above 12 mg • L^{-1} throughout the river length and at Lillooet a value of 16 mg • L^{-1} is given for the November–December period of 1975 (Clark et al. 1981), indicating supersaturation. Dissolved oxygen concentrations of course are highest in winter and lowest in summer (Fig. 8), following largely thermal effects on solubility.

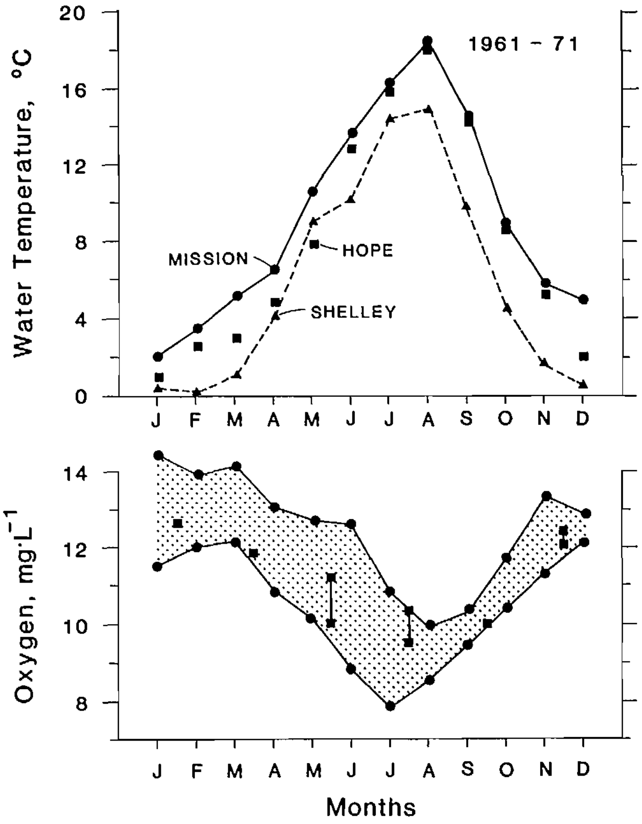


FIG. 8. *Upper:* seasonal changes in average monthly water temperature (mainly 1961–71) at three stations on the mainstem Fraser River.
Lower: seasonal changes in monthly (Mission 1961–71) or bimonthly (Shelley 1975) range in dissolved oxygen at tow stations on the mainstem Fraser River.

Heavy Metals and Organic Contaminants

Although the pattern is far from clear or consistent, concentrations of four dissolved heavy metals attain highest concentrations in the arms of the lower reaches (Table 4). Concentrations of copper, lead and zinc are orders of magnitude higher in sediments and biota compared to levels in the river water itself. The greater concentrations in the sediments presumably reflect the adsorption of heavy metals on silt particles, and that in the biota reflect uptake and accumulation during residence in the bottom sediments. Maximum copper and zinc levels in bivalves and crustaceans considerably exceed levels set for human food. In crabs and in six of the 14 fish species tested for mercury at least some individuals exceed the 0.5 ppm limit. There is no regional pattern in heavy metal load in fish muscle, except perhaps for lead where highest amounts are found in individuals from the river arms compared to those in the mainstem between New Westminster and Hope.

The sources of the heavy metals in the sediments and biota include effluent discharges from metal plating and similar industries, together with street washings from urbanized areas (Hall et al. 1976). Some of the lead may originate from the activities of waterfowl hunters.

Levels of most organic contaminants checked in Fraser River water were below detection limits (Hall et al. 1974;

TABLE 4. Maximum concentration of four heavy metals in water, bottom sediment, invertebrates and fish from the Fraser River system.

Metal	Source	Authority	Arms, Banks	Region		
				Lower	Mid	Upper
Copper (100 p.p.m.)[b]	**Water** μg • L^{-1}	Benedict et al. (1973)	52	65		
		Hall et al. (1974)	14	10		
		Whitfield, unpubl. data[c]			30	7
		Clark et al. (1981)	6	10	26	14
	Sediment μg • g^{-1} dry wt.	Geesey et al. (1984)		64		
	p.p.m. dry wt.	Grieve and Fletcher (1976)	19.8			
		Rocchini et al. (1979)	26[a]	28[a]		
	Attached Algae p.p.m. dry wt.	Rocchini et al. (1979)	50[a]	46[a]		
	Annelids & Insects p.p.m. dry wt.	Bawden et al. (1973)	20			
		Rocchini et al. (1979)	16–38[a]	44[a]		
	Bivalves **Crabs** **Shrimp** p.p.m. dry wt.	Bawden et al. (1973)	400 150 400			
	Fish p.p.m. wet wt.	Northcote et al. (1975b)	1.2	1.5		
Lead (10 p.p.m.)[b]	**Water** μg • L^{-1}	Benedict et al. (1973)	34	4		
		Hall et al. (1974)	33	4		
		Whitfield, unpubl. data			20	8
		Clark et al. (1981)	4	8	5	5
	Sediment p.p.m. dry wt.	Grieve and Fletcher (1976)	5.8			
		Rocchini et al. (1979)	8.6[a]	7.6[a]		
	Attached Algae p.p.m. dry wt.	Rocchini et al. (1979)	55[a]	51[a]		
	Annelids & Insects p.p.m. dry wt.	Bawden et al. (1973)	<2.0			
		Rocchini et al. (1979)	6–11[a]			
	Bivalves **Crabs** **Shrimp** p.p.m. dry wt.	Bawden et al. (1973)	<2.0 <2.0 <2.0			
	Fish p.p.m. wet wt.	Northcote et al. (1975b)	0.9	<0.2		
Zinc (100 p.p.m.)[b]	**Water** μg • L^{-1}	Benedict et al. (1973)	32	1		
		Hall et al. (1974)	80	27		
		Whitfield, unpubl. data[c]			30	25
		Clark et al. (1981)	100	11	120	80
	Sediment p.p.m. dry wt.	Grieve and Fletcher (1976)	57			
		Rocchini et al. (1979)	85[a]	72[a]		
	Attached Algae p.p.m. dry wt.	Rocchini et al. (1979)	185[a]	153[a]		

TABLE 4. *(Continued)*

Metal	Source	Authority		Region		
			Arms, Banks	Lower	Mid	Upper
	Annelids &	Bawden et al. (1973)	95			
	Insects p.p.m. dry wt.	Rocchini et al. (1979)	175[a]	165[a]		
	Bivalves	Bawden et al. (1973)	2 400			
	Crabs		290			
	Shrimp p.p.m. dry wt.		130			
	Fish p.p.m. wet wt.	Northcote et al. (1975b)	21.0	14.0		
Mercury (0.50 p.p.m.)[b]	**Water** $\mu g \cdot L^{-1}$	Benedict et al. (1973)		N.D.[d]		
		Hall et al. (1974)	0.40	0.07		
		Clark et al. (1981)	<0.85	0.26	0.90	0.38
	Sediment p.p.m. dry wt.	Rocchini et al. (1979)	0.29[a]			
	Attached Algae p.p.m. dry wt.	Rocchini et al. (1979)	0.09[a]	0.14[a]		
	Annelids &	Bawden et al. (1973)	0.11			
	Insects p.p.m. dry wt.	Rocchini et al. (1979)	0.82[a]			
	Bivalves	Bawden et al. (1973)	0.46			
	Crabs		3.70			
	Shrimp p.p.m. dry wt.		0.14			
	Fish p.p.m. wet wt.	Northcote et al. (1975b)	1.4	2.2		

[a] Average values.

[b] Maximum concentrations (wet or "marketed" weight) permitted in products for human consumption (Can. Dep. Food Drug Stand.); divide values for crab and shrimp by 5 and bivalves by 20 for comparison.

[c] Water Quality Branch, Inland Waters Directorate, Environment Canada, 502–1001 W. Pender St., Vancouver, B. C.

[d] Not detected.

Garrett 1980) but some, such as the chlorinated phenols used as wood preservatives, have been found in water samples near chemical manufacturing plants and lumber mills. Various chlorinated hydrocarbons have been detected in the sediments of urban–industrial tributaries draining into the lower reaches of the Fraser (Hall et al. 1976) but the concentrations in mainstem river sediments appeared to be generally low except in localized areas (Garrett 1980). Nevertheless, significant levels of several chlorinated hydrocarbons were found in shellfish, crabs and fish from the lower Fraser and greatest concentrations for several compounds occurred in biota from waters adjacent to the city of Vancouver (Johnston et al. 1975; Albright et al. 1975). Although considerable data are available on toxic contaminants in the lower Fraser River system, much of this information comes from the early 1970s and very much needs updating with better analytical techniques and selective broader coverage (Hall 1986).

Possible contamination of mainstem Fraser and Thompson river water by pulpmill discharge has been of concern since the mid 1960s (Servizi et al. 1968) and continues to be so (Birtwell et al. 1986). Although other problems remain, no detectable levels of chlorinated hydrocarbons or resin acids could be found in fish utilizing the mainstem river near Prince George where wastes were released (Rogers and Mahood 1982).

Coliform Bacteria

Water quality of the Fraser mainstem, as expressed by coliform bacterial load (Table 5), shows an obvious change along its length. Near its source, coliform bacteria counts (both total and fecal) are low but they increase sharply even within the upper reach stations. This trend continues in the middle reach stations but it is not until New Westminster in the lower reach that counts of 10 000 total and 6 000 fecal are exceeded. Although no obvious seasonal trend appears in the available data, Churchland and Kan (1982) demonstrate significant diel variation in fecal coliform counts depending on tidal cycle and location of sampling stations in relation to major sewage outfalls on the lower Fraser River.

TABLE 5. Summary of regional coliform bacterial load[a] in the mainstem Fraser River.

Reach	Station	Year	Total coliform		Fecal coliform	
Upper	Red Pass	1975	13	(9)	2	(9)
	McBride	"	79	(9)	11	(9)
	Hansard	"	79	(6)	23	(6)
	Shelley	"	540	(10)	49	(10)
Mid	Red Rock	1975	2 400	(10)	240	(10)
	Lillooet	"	2 400	(20)	1 700	(20)
	Hope	1973	3 300	(7)	490	(7)
	"	1975	9 200	(22)	5 400	(23)
Lower	Mission	1973	3 500	(7)	3 100	(7)
	"	1975	9 200	(23)	5 400	(24)
	New Westminster	1952–71	110 000	(>24)	—	—
	"	1973	54 000	(8)	7 900	(7)
	"	1975	9 200	(21)	2 400	(25)
	Arms	1952–71	430 000	(>48)	—	—
	"	1973	92 000	(37)	79 000	(33)
	"	1975	54 000	(87)	24 000	(104)

[a] Most probable number per 100 mL, maximum recorded; 1952–71 data from Benedict et al. 1973, 1973 data from Hall et al. 1974, 1975 data from Clark et al. 1981; numbers in parentheses give sample size.

Bacterial, Algal, and Macrophytic Producers

Bacterial Dynamics

The key role of bacteria in production processes of lower Fraser marshes has been well reviewed by Kistritz (1978), though rates and contributions of the various pathways clearly need quantification. Virtually all such work has been restricted to the lower Fraser, its estuary, and adjacent coastal waters. Over a decade ago, Oloffs et al. (1972) showed that bacterial plate counts for Fraser water from New Westminster were of the same order of magnitude as those for a coastal site in the Strait of Georgia. More recently, Bell and Albright (1981) demonstrated a decline in both total and free-floating bacterial counts (epifluorescent) between New Westminster (total > 6 million cells • mL^{-1}) and a station about 10 km from the river mouth. Further downstream an increase to about 6 million cells • mL^{-1} occurred, largely because of the free-floating component. About 60 % of the bacterial biomass and heterotrophic activity was associated with suspended particulates in the turbid Fraser River water near New Westminster, but the contribution of attached bacteria decreased to less than 40 % of total numbers and 4 % of heterotrophic activity in the Strait of Georgia (Bell and Albright 1981). Bacterial heterotrophic potential was highest during winter and early spring, whereas productivity was maximal during summer and autumn in the lower Fraser (Albright 1977). Compared to photosynthetic production, that coming from bacterial contributions was highest in the river, intermediate in the plume off the river mouth, and lowest in the strait (ratios of 3.1:1, 0.6:1 and 0.25:1, respectively (Bell and Albright 1981)).

Algal Producers

Apart from the chrysophyte *Dinobryon*, most planktonic algae in lower Fraser waters are diatoms (Northcote et al. 1975a) with forms such as *Melosira italica* and *Tabellaria fenestrata* being well represented. Cell densities are highest in spring, especially in the mainstem between New Westminster and Hope (usually 200–400 cells • mL^{-1}) and decrease to levels below 100 cells • mL^{-1} in summer and autumn. The seasonality in phytoplankton abundance evident in the lower Fraser does not seem to be so clearly related to discharge, nutrients and water transparency as in some large rivers such as the Danube (Welcomme 1985).

Diatom dominance is a common feature for the phytoplankton of large rivers (Blum 1956; Cushing and Rancitelli 1972) but is rarely so complete as in the lower Fraser River. The only large, turbid river close to the Fraser whose phytoplankton has been examined in detail is the Columbia (Cushing and Rancitelli 1972; Williams 1964, 1972; Williams and Scott 1962) but its planktonic flora may be atypical because of the many sizeable impoundments. Nevertheless, of the 11 principal diatom species in its waters, all but one are also common in the lower Fraser River. Phytoplankton density in the Fraser is consistently below that in the Columbia where medial counts range from nearly 400 to over 1000 cells • mL^{-1} (Williams and Scott 1962) and very much less than in the Thames where spring peaks may exceed 70 000 cells • mL^{-1} (Lack 1971). High discharge and turbidity combined with the lack of any significant mainstem lakes or impoundments may be factors contributing to low phytoplankton density in the Fraser River.

Phytoplankton production rates in the estuary at the river mouth are maximal in the spring to summer and minimal in autumn to winter (range 60–380 • 10^{-4} mg C • L^{-1} • d^{-1}) with a mean value of 156 • 10^{-4}, slightly above that of 142 • 10^{-4} for bacterial plankton (Albright 1977). Unfortunately, areal rates do not seem to be available for comparison with other large rivers, but the vertical production profile, considering the light transmission curves given by Northcote et al. (1975a), must follow at least as thin a layer as that shown for Amazonian floodplain waters (see Welcomme 1985, fig. 3.2, table 3.1).

The attached algal community (periphyton) of the Fraser

River has been examined mainly on wood surfaces in its lower reaches (Northcote et al. 1975a). Obvious concentration zones of attached algae formed just below the water line at most stations in the river arms, but further upstream only thin algal films appeared in patches. Total periphytic biomass approached 20 mg • cm^{-2} in the arms but rarely exceeded 6 mg • cm^{-2} at upstream stations, well below that reported as the annual maximum (650 g • m^{-2}) for the Danube (Ertl et al. 1972). Diatoms were the dominant group, being represented by some 112 species of which only 20 were common. Green algae (22 species, 11 common) were the second most abundant group and together with diatoms accounted for virtually all of the periphyton. Both periphyton biomass and cell density (7–12 million cells • cm^{-2} at North Arm stations, 0.5–4.5 million cells • cm^{-2} elsewhere) in the lower Fraser were high in comparison to those of many other rivers. Periphytic production rates have not been measured in the Fraser River proper, but in the arms could be high in local concentration zones. However, because of the severe light limitation, production would not be so high over most of the bottom.

Pomeroy and Levings (1980) recorded 13 species of benthic algae associated with rock surfaces of Fraser River mouth jetties, *Enteromorpha linga* being most widespread with a mean biomass of 135 g • m^{-2} dry wt (about 54 g C • m^{-2}). On nearby sandflat habitat, mean biomass values of benthic microalgae were 0.67 g C • m^{-2} in January and 0.89 g C • m^{-2} in August 1978.

Macrophyte Producers

In low profile regions of the upper Fraser (Fig. 4) macrophytes must have local importance in contributing to overall primary production in river backwaters, meanders and oxbows but this has not been studied. In the middle reach canyons and throughout the now largely dyked lower reaches of the river, macrophytic contribution to primary production must be low although again unmeasured. Only in the Fraser estuary are there extensive marshes (Kistritz 1978) with a total existing area estimated at 27 km^2. Four tidal marsh communities are recognized by the dominant species: *Typha, Carex, Scirpus* and the "saltmarsh" (*Salicornia, Distichlis, Triglochin*). Average dry matter standing crop and primary production have been estimated for eight major species with one (*Carex lyngbyei*) producing almost twice the standing crop of the other seven combined (Yamanaka 1975). Dry matter yields in the tidal marsh range up to 1 819 g • m^{-2} • y^{-1} with an average for 1974 of 490 and 580 g • m^{-2} • y^{-1} for the two bank areas at the river mouth (Yamanaka 1975) and 850 g • m^{-2} • y^{-1} for inner marshes of the Main Arm (Kistritz 1978).

About 70 % of the historic wetlands on the estuarine and floodplain system have been lost, most by early dyking but in part by recent development (Anon. 1978). Nevertheless in some parts of the inner estuary there has been a substantial increase in marsh area over historic quantities (M.E.A. North, Geography Department, Univ. Brit. Col., pers. comm.).

Drift and Benthic Invertebrates

Drift Fauna

The invertebrate drift fauna of the lower Fraser River was sampled at 14 near shore and mid river stations at 3 or 4 periods between the summer of 1972 and 1973 using coarse (1.18 mm) and fine (0.35 mm) mesh tow nets (Northcote et al. 1976). The coarse net captured mainly insect larvae and adults with smaller amounts of benthic crustaceans and other invertebrate forms usually associated with the bottom. Densities averaged about one organism per 100 m^3 at all of the stations with no consistent regional or seasonal trend. The fine net captured mainly small planktonic cladocerans and copepods whose densities increased about 10-fold between Hope and the estuary (Fig. 9).

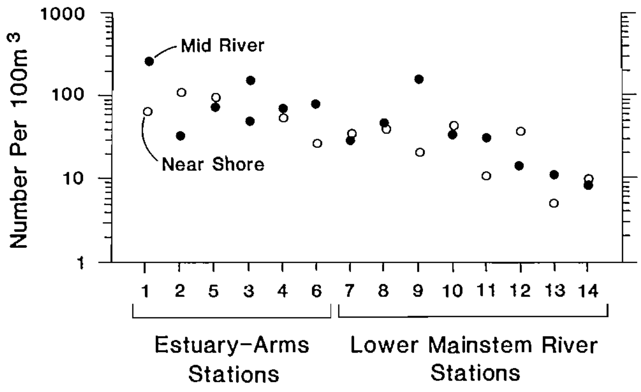


FIG. 9. Seasonal average density of invertebrate drift sampled with a 0.5 m (0.35 mm mesh) tow net at 14 stations along the mainstem lower Fraser River, 1972–73. Adapted from Northcote et al. 1976; Stations 1,2,5 in North Arm; 3,4,6 in Main Arm; 7–14 from New Westminster to near Hope.

Epibenthic Fauna

The biomass of epibenthic invertebrates increased from an average of about 1 mg • m^{-2} in the mainstem lower reaches below Hope to levels well over 100 mg • m^{-2} in the estuarine arms near the river mouth (Fig. 10). At the upper stations (> 100 km from the river mouth) non-dipteran insect larvae and nymphs made their highest contribution to epibenthic biomass and, along with dipteran larvae as well as low amounts of oligochaetes, made up the greatest part of the fauna. *Neomysis mercedis*, a common epibenthic invertebrate of the lower Fraser, first appeared in the samples about 100 km from the river mouth (average biomass ca 10 mg • m^{-2}), and from the next station downstream to the mouth, contributed averages ranging from 10 to 1000 mg • m^{-2} to the total biomass (Northcote et al. 1976). Non-dipteran larvae and nymphs declined sharply in the river arms, being virtually absent from North Arm stations. By contrast, amphipods, molluscs, shrimp and polychaete worms were largely restricted to the river arms, reaching their highest contribution at or near the mouth. Oligochaete worms, largely tubificids, reached maximum abundance and biomass at the North Arm stations.

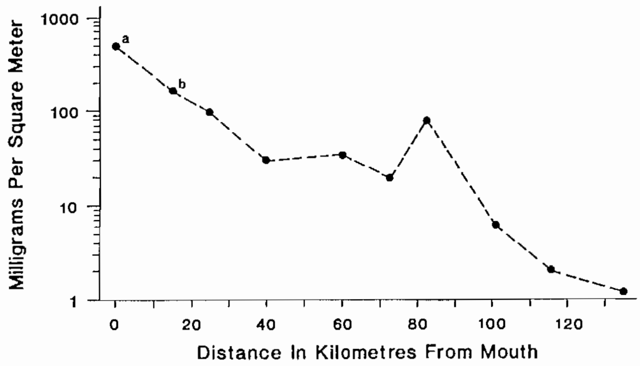


FIG. 10. Average biomass of epibenthic invertebrates taken in bottom tows at stations along the mainstem lower Fraser River, 1972–73; adapted from Northcote et al. 1976. [a]stations 1–4 at mouth of arms averaged; [b]stations 5 and 6 in North and Main arms averaged.

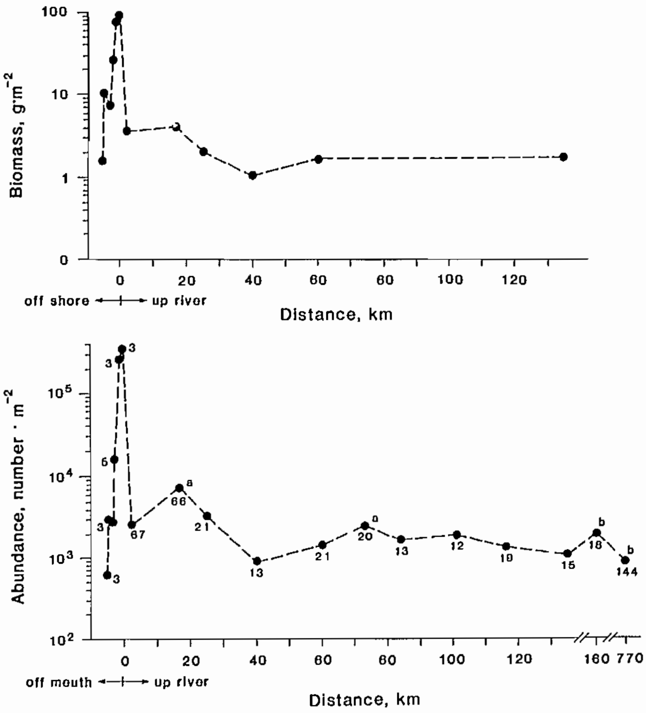


FIG. 11. Average abundance and biomass of benthic invertebrates in mud and mud-sand bottom of the Fraser River system from Sturgeon Bank off the river mouth (Levings and Coustalin 1975 data), up the arms (combined data, Northcote et al. 1976), and the mainstem river, 1972–73. Numbers beneath abundance data points give number of Petersen dredge samples. [a]includes six samples from Servizi and Burkhalter (1970); [b]1963–65 data from Servizi and Burkhalter (1970).

Benthic Fauna

Extensive sampling of benthic invertebrates of the Fraser River was initiated by Servizi and Burkhalter (1970) mainly in the middle reaches and followed by Stone et al. (1974) and others more recently (e.g., Dwernychuk 1984), and in the lower reaches by Northcote et al. (1976). In the lower mainstem river and the middle reaches near Prince George, nearly 800 km upstream, the average density of benthic invertebrates on mud or mud-sand bottom ranges between about 1000 and 3000 organisms per m^2 (Fig. 11). Only in the estuarine arms does average abundance begin to increase appreciably, with a very sharp peak of over 10 000 organisms per m^2 just off the river mouth followed by a decline further offshore to numbers lower than anywhere sampled in the mainstem river. This pattern in abundance is closely followed by that in biomass (Fig. 11), and by a similar spike in both abundance and biomass at Roberts Bank (Levings and Coustalin 1975). Regional changes in faunal composition noted previously for epibenthic invertebrates also apply to the benthic fauna; see Northcote et al. (1976) for details. Although seasonal shifts occur in the benthic invertebrate fauna of the estuarine portion of the lower reaches (Chapman and Brinkhurst 1981), their study shows densities similar to those of Northcote et al. (1976).

Pollution "tolerant" and "sensitive" invertebrates change markedly in the lower 60 kilometers of the Fraser River (Fig. 12). Further upstream these two groups are about equally abundant, but downstream the contribution of the pollution sensitive group declines sharply whereas that of the tolerant group increases. Tolerant forms reach maximum abundance and sensitive forms minimum abundance in the North Arm. These changes may not be solely related

TABLE 6. Comparison of benthic macroinvertebrate density (average numbers per m^2) sampled by Petersen dredging on mud bottom of the mainstem Fraser River above, between and below pulp mills at Prince George, British Columbia. Number of samples given in parentheses; organisms grouped into three pollution tolerance groups after Servizi and Burkhalter (1970).

Years	Above pulp mills				Between pulp mills				Below pulp mills			
	Sensitive	Facultative	Tolerant	Total	Sensitive	Facultative	Tolerant	Total	Sensitive	Facultative	Tolerant	Total
1963–'65[a]	0	128.8*	156.6	285.4 (5)[d]	7.4	1030.1	541.9	1579.4 (9)[d]	6.6	417.0	23.4	447.0 (10)[d]
1966–'70[b]	—	—	—	—	19.4	389.6	174.4	583.4 (5)	24.0	398.5	1277.3	1699.8 (10)
1972–'75[c]	8.5	658.3*	92.4	759.2 (24)	15.0	357.1	272.4	644.5 (24)	5.0	697.3	12.1	714.4 (31)

[a] Data from Servizi and Burkhalter (1970)

[b] Data from Stone et al. (1974); only averages are available.

[c] Data from IEC Beak Consultants Ltd. Reports.

[d] Number of composite samples with 6 dredgings per sample.

* Significant difference @ $P < 0.05$, t-tests with $\sqrt{x + 0.5}$ transformed data.

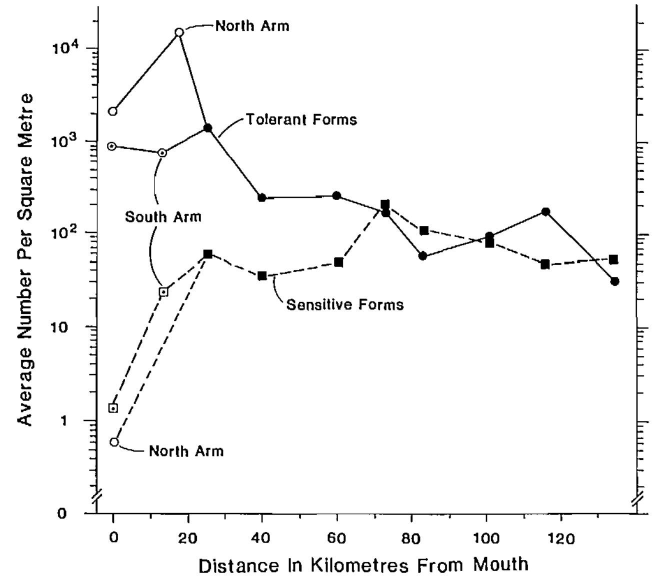


FIG. 12. Changes in abundance of pollution tolerant and sensitive groups of benthic macroinvertebrates in the lower Fraser River. Adapted from Northcote et al. (1976); see for details.

to pollution as the complicating effects of estuarine salinity must be considered (Northcote et al. 1976). Mercury accumulations nearly four times above sediment levels occur in two species of tubificid oligochaetes from the North Arm and the mainstem Fraser near New Westminster (Chapman et al. 1980).

Petersen dredge sampling of mud substrate has been continued at three stations (above, between and below the Prince George) on the mainstem Fraser River for about a decade after pulp mill start-up in the mid 1960s. Individual sample counts at these stations permit statistical comparison of macroinvertebrate densities (Table 6) between the before (1963-65) and after (1972-75) periods of pulp mill operation. Like most benthic data, variability between samples is high so that despite large differences between mean values, only in one case (pollution facultative organisms, above pulp mill station) could a significant difference be demonstrated. Otherwise, there were no significant differences in benthic invertebrate densities on mud bottom between stations or before and after pulp mill operation, a conclusion consistent with other reports (Derksen 1981).

Additional data on macrobenthic invertebrates of the mainstem Fraser River are available from colonization traps placed on gravel or rubble bottom near Prince George in the upper portion of the middle reaches and at Mission in the lower reaches (Table 7). Although the total numbers of invertebrates colonizing the trays were significantly less at the Prince George sites compared to the Mission site, the former locations had a significantly higher proportion of pollution sensitive forms. In contrast, forms considered facultative of polluted conditions were significantly more abundant at Mission, about the centre of the lower reaches of the river. A long series of benthic sampling with trays has been conducted in the mainstem Fraser River to assess effects of Prince George pulp mill effluents. Unfortunately, changes in tray design, in screen sizes used to sort the fauna and other complications make interpretation of the data difficult but no major deleterious shifts in the benthic community appear to have occurred away from the immediate outfall sites (Dwernychuk 1984).

Fraser River System Fishes

Preglacial Fishes

Although it is not clear that the major valley of the Fraser system was present as early as the middle Eocene, there is no doubt that a moderately diverse freshwater fish fauna existed well over 40 million years ago in the region now occupied by its watershed (Wilson 1977a,b, 1980, 1984). Fish-bearing horizons also have been identified in upper Eocene, lower Oligocene and lower Pliocene deposits along the mainstem Fraser River or some of its major tributaries such as the Thompson and Quesnel rivers (Wilson 1977a).

Representatives from at least five families of freshwater fishes have been recorded, including amiids, hiodontids, probably the salmonid *Eosalmo*, several catostomids, and a priscacarid (Wilson 1977a). The probable Eocene lake environments and their fish associations include (1) a littoral assemblage with abundant small hiodontids, catostomids and large amiids, (2) an intermediate depth assemblage with

TABLE 7. Comparison of benthic macroinvertebrates colonizing trays (900 cm^2, 30 days) placed on gravel-rubble bottom (1.8 – 4.6 m depth) in mainstem Fraser River, 1963-66.[a]

Location	*n*	Average % Pollution Sensitive	Average Number Per m^2 Pollution			Total
			Sensitive	Facultative	Tolerant	
Prince George[b]	11	79.5	229.5	34.6	2.4	266.5
Mission	10	62.8	323.5	181.7	5.1	510.3
t-test value, comparison for significant difference[c]		2.093^{*c}	1.797	2.093^{*}	1.760	2.118^{*}

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[a] Data from Servizi and Burkhalter (1970); all tests with $\sqrt{x}$ transformation except where noted otherwise.

[b] Combined from upstream, between and downstream of future pulpmill sites after demonstrating no significant differences between sites ($\sqrt{x}$ transformation), $P < 0.05$.

[c] arc sin $\sqrt{}$transformation.

* $P < 0.05$.

abundant hiodontids and salmonids, and (3) a deep limnetic assemblage of low diversity dominated by large catostomids (Wilson 1977b, 1980).

A much more diverse fish fauna (22 genera from seven families) has been recorded (McPhail and Lindsey 1986) from Late Cenozoic deposits within "Cascadia" (Columbia, Fraser, Skeena, Stikine, and adjacent river systems) but it is not clear how many of these might have occurred within the Fraser area itself. Interestingly, the salmonids are represented by six genera, two of which are extinct (*Rhabdofario, Smilodonichthys*), one of which is extinct in Cascadia but present in Eurasia (*Hucho*) and three of which now are common in the Fraser system (*Oncorhynchus, Prosopium, Salmo*).

Postglacial and Present-Day Fishes

The postglacial re-invasion of fishes into freshwaters forming the Fraser watershed has been recently considered by McPhail and Lindsey (1986). At least four distinct invasion routes are evident: (1) from the Columbia River system either by postglacial lake connections in the Okanagan–Nicola areas noted previously, or by upper mainstem Columbia connections; (2) from the Mississippi River system via middle-upper Fraser postglacial lake connections through the Peace–Mackenzie rivers (Lindsey and McPhail 1986); (3) from the Chehalis River (Washington) system by lower Fraser postglacial lake connections; and (4) from the Pacific Ocean either by marine submergence and re-emergence (e.g. the "landlocked" *Spirinchus thaleichthys* populations in Pitt and Harrison lakes) or by direct entry of euryhaline species. At least 10 euryhaline species which re-entered the Fraser system from the sea (including three salmonines — *Salmo clarki clarki, Oncorhynchus keta, Salvelinus malma*) — are largely confined to its lower reaches and have not made their way into the upper reaches presumably because of velocity barriers in the Fraser Canyon (McPhail and Lindsey 1986).

Today there are at least 53 species of fish known to occur in the Fraser River and its tributary waters. Six of these have been introduced by man within the last century either directly (*Salvelinus fontinalis, Carassius auratus, Lepomis gibbosus*), inadvertently, or by spread from other sites of introduction (*Alosa sapidissima, Cyprinus carpio*). Of the 47 native species, seven are normally considered marine species which might only have been taken during brief excursions into the mouths of the river arms. This surely must be the case for *Clupea harengus, Microgadus proximus, Synchirus gilli* and perhaps for *Cymatogaster aggregata*. Juveniles and adults of *Hypomesus pretiosus* and *Leptocottus armatus* are regularly taken from full freshwater in considerable numbers, chiefly in the estuarine arms. *Platichthys stellatus* occurs in the mainstem river as far upstream as Mission. Therefore, not counting marine "strays", the fish fauna of the Fraser system is composed of at least 41 freshwater species and three marine species that regularly enter the arms or lower reaches.

There are 14 families represented in the Fraser fish fauna, most (10) with three or less species (Table 8). Salmonids dominate the assemblage with 14 species (11 of which are salmonines), followed by cyprinids, cottids and catostomids. Neglecting introductions, the estuarine reaches have the highest species richness (34), followed by the lower (33) and upper (29) reaches.

The general biological features of the lower Fraser River fishes have been reviewed previously (Northcote 1974) with additional information on species which migrate to middle or upper reaches. Subsequently there have been several studies on the use of estuarine habitat and food resources by juvenile salmon (Levy et al. 1979; Levy and Northcote 1981, 1982; Levings 1982) as well as by other fishes (Gordon and Levings 1984). In addition, the distribution, abundance, size and feeding relationships of lower Fraser fishes have been studied (Northcote et al. 1978; 1979) as have special features of some species such as chum salmon (Beacham and Starr 1982), pink and sockeye salmon (Cooper 1977; Gilhousen 1980), as well as coho and chinook salmon (Delaney et al. 1982; Fraser et al. 1982). The population dynamics of the white sturgeon from the time it was first harvested for isinglass at the turn of the century were reconstructed by Semakula and Larkin (1968). Recent data on headwater populations of white sturgeon are now available (Dixon 1986).

Although investigations of lamprey biology in the lower Fraser River are underway, far too little is known of these species, at least two of which are predaceous on salmon. Lamprey ammocoetes form a significant part of the benthic community of the mainstem lower Fraser, particularly so in terms of biomass (Northcote et al. 1976), so their potential impact on salmonid populations should not be ignored. Off the Fraser River mouth, river lamprey (*Lampetra ayresi*) feed far more intensively on herring than on salmon (Beamish and Scarsbrook 1979).

Salmonine Diversity and Production

Although the Fraser River in its size (length) ranks only 28th out of 39 large rivers of the world which support either native or introduced salmonine fishes, there is little doubt about its high position in terms of salmonine species richness (Table 9) and relative abundance (Table 10). There are about 32 species of salmonine fishes (Nelson 1984) and most of these occur in the watersheds of large rivers with only the three species of *Salmothymus* being obvious exceptions. With respect to the native salmonines, the Fraser and Skeena rivers share top place with the same ten species in each (Table 9). The Sacramento–San Joaquin, Columbia, Yukon and Mackenzie rivers follow closely with nine each. Apart from the Amur River with eight native salmonines, all other large systems with salmonines have five or fewer species and eight of these — including the two largest rivers (Nile, Amazon) — have no native salmonines. Even with the addition of introduced species, the salmonine richness of the Fraser is only exceeded by the Columbia and Mackenzie river systems as a result of localized introductions of non-native salmonines (four and three species, respectively).

A subset of 13 large river basins was used to examine relative abundance of salmonine fishes in comparison to that of the Fraser system (Table 10). Most of the large North American rivers were included along with four in Eurasia. *Salvelinus malma* and *S. confluentus* were grouped together because they have been confounded in most catch and stock records. A seven step "order of magnitude" scale of relative abundance was used to categorize both anadromous and resident stocks of the species, drawing on available publica-

TABLE 8. Fishes of the Fraser River system showing regional distribution. Numbers in parentheses give introduced species included in totals. Data in part from McPhail and Lindsey (1986).

Family	Species	Common name	Estuarine Arms[a]	Lower Fraser[b]	Mid-upper Fraser[c]	Species Total per family
Petromyzonidae	*Lampetra ayresi*	River lamprey	+	+		
	L. richardsoni	Western brook lamprey	+	+		3
	L. tridentata	Pacific lamprey	+	+	+	
Acipenseridae	*Acipenser medirostris*	Green sturgeon	+	+		
	A. transmontanus	White sturgeon	+	+	+	2
Clupeidae	*Alosa sapidissima*	American shad	i	i		2
	Clupea harengus	Pacific herring	+			
Salmonidae	*Coregonus clupeaformis*	Lake whitefish		i	+	
	Prosopium coulteri	Pygmy whitefish			+	
	P. williamsoni	Mountain whitefish	+	+	+	
	Salvelinus confluentus	Bull trout	+	+	+	
	S. fontinalis	Brook trout		i	i	
	S. malma	Dolly Varden	+	+		
	S. namaycush	Lake trout			+	14
	Salmo clarki	Cutthroat trout	+	+		
	S. gairdneri	Rainbow trout	+	+	+	
	Oncorhynchus gorbuscha	Pink salmon	+	+	+	
	O. keta	Chum salmon	+	+		
	O. kisutch	Coho salmon	+	+	+	
	O. nerka	Sockeye salmon	+	+	+	
	O. tshawytscha	Chinook salmon	+	+	+	
Osmeridae	*Hypomesus pretiosus*	Surf smelt	+			
	Spirinchus thaleichthys	Longfin smelt	+	+		3
	Thaleichthys pacificus	Eulachon	+	+		
Cyprinidae	*Acrocheilus alutaceus*	Chiselmouth			+	
	Carassius auratus	Goldfish		i	i	
	Couesius plumbeus	Lake chub			+	
	Cyprinus carpio	Common carp	i	i	i	
	Hybognathus hankinsoni	Brassy minnow	+	+	+	
	Mylocheilus caurinus	Peamouth	+	+	+	10
	Ptychocheilus oregonensis	Northern squawfish	+	+	+	
	Rhinichthys cataractae	Longnose dace		+	+	
	R. falcatus	Leopard dace	+	+	+	
	Richardsonius balteatus	Redside shiner	+	+	+	
Catostomidae	*Catostomus catostomus*	Longnose sucker		+	+	
	C. columbianus	Bridgelip sucker		+	+	
	C. commersoni	White sucker			+	5
	C. macrocheilus	Largescale sucker	+	+	+	
	C. platyrhynchus	Mountain sucker		+	+	
Ictaluridae	*Ictalurus nebulosus*	Brown bullhead	i	i		1
Gadidae	*Lota lota*	Burbot		+	+	2
	Microgadus proximus	Pacific tomcod	+			
Gasterosteidae	*Gasterosteus aculeatus*	Threespine stickleback	+	+		1
Cottidae	*Cottus aleuticus*	Coastrange sculpin	+	+		
	C. asper	Prickly sculpin	+	+	+	
	C. cognatus	Slimy sculpin			+	6
	C. rhotheus	Torrent sculpin			+	
	Leptocottus armatus	Pacific staghorn sculpin	+			
	Synchirus gilli	Manacled sculpin	+			
Centrarchidae	*Lepomis gibbosus*	Pumpkinseed		i		
	Pomoxis nigromaculatus	Black crappie	i	i		2
Embiotocidae	*Cymatogaster aggregata*	Shiner perch	+			1
Pleuronectidae	*Platichthys stellatus*	Starry flounder	+	+		1
Total	53 (7)		37 (4)	40 (8)	32 (3)	

[a] From New Westminster to mouths of arms (North, Middle, Main, Canoe Pass).
[b] From Hope to New Westminster.
[c] Upstream from Hope.

TABLE 9. Salmonine fishes[a] in some large river basins of the world.[bc]

Region	River basin	Length (km)	Rank	Minor genera		*Salvelinus*						*Salmo*					*Oncorhynchus*						Totals		
				B.	H.[a]	al	fo	ma	co	na	le	sa	tr	cl	ga	ag	go	ke	ki	ne	ts	ma	+	*i*	
North America	Sacramento-S.J.	673;563	38				i	+	+				i		+	+	+	+	+	+	+		9	2	11
	Columbia	2000	23				i	+	+	i			i	+	+	i	+	+	+	+	+		9	4	13
	Fraser	1375	28				i	+	+	+				+	+		+	+	+	+	+		10	1	11
	Skeena	579	39				i	+	+	+				+	+		+	+	+	+	+		10	1	11
	Yukon	3185	13			+		+	+	+				i	i		+	+	+	+	+		9	2	11
	Mackenzie	4241	9			+	i	+	+	+			i	i	+		+	+		+	+		9	3	12
	Churchill	1609	26			+	+			+					i								3	1	4
	Nelson	2575	20			+	+		+	+			i	+	i	i							5	3	8
	St. Lawrence	3058	15			+	+			+		+	i	i	i		i		i	i	i		4	7	11
	Missouri-Mississippi	6418	2				+			+			i	+	i	i				i	i		3	5	8
Eurasia	Loire	1006	32									+	+		i								2	1	3
	Seine	772	35									+?	+		i								2?	1	3
	Rhine	1320	29			+	i					i[e]	+		i								2	3	5
	Elbe	1167	30				i								i								0	2	2
	Oder	885	33				i					+	+		i								2	2	4
	Vistula	1046	31		i		i						+		i								1	3	4
	Sev. Dvina	756	37	+	+							+	+										4	0	4
	Ob	4023	10	+	+																		2	0	2
	Yenisei	4506	7	+	+	+																	3	0	3
	Lena	4506	6	+	+	+											+	+					5	0	5
	Kolyma	1609	27	+		+											+	+					4	0	4
	Amur	4345	8	+	+			+			+						+	+		i	+	+	8	1	9
	Yellow	4506	5	+	i										i[d]								1	2?	3
	Yangtze	5150	4		+										i[d]								1	1?	2
	Brahmaputra	2736	17										i										0	1	1
	Indus	3058	14										i		i								0	2	2
	Volga	3742	12										+		i								1	1	2
	Don	1931	24										+										1	0	1
	Dnieper	2253	21		+								+		i								2	1	3
	Danube	2776	16		+	+	i						+		i								3	2	5
	Rhone	811	34			+?							+		i								2?	1	3
	Ebro	756	36				i								i								0	2	2
Africa	Nile	6437	1												i								0	1	1
	Zambeze	2655	18										i		i								0	2	2
	Orange	2092	22										i		i								0	2	2
South America	Orinoco	2575	19				i								i								0	2	2
	Amazon	6276	3												i								0	1	1
	Parana	3943	11												i								0	1	1
Australia	Murray	1931	25										i		i								0	2	2

[a] B. = *Brachymystax lenok*, H. = *Hucho spp.* (3–5), al = *Salvelinus alpinus*, fo = *S. fontinalis*, ma = *S. malma*, co = *S. confluentus*, na = *S. namaycush*, le = *S. leucomaenis*, sa = *Salmo salar*, tr = *S. trutta*, cl = *S. clarki*, ga = *S. gairdneri*, ag = *S. aguabonita*, go = *Oncorhynchus gorbuscha*, ke = *O. keta*, ki = *O. kisutch*, ne = *O. nerka*, ts = *O. tshawytscha*, ma = *O. masou*.

[b] + native, i introduced.

[c] Assembled from various sources including Andriyashev (1954), Arrignon (1972), Balon et al. (1986), Berg (1949), Brenner (1984), Burr and Page (1986), Busnita (1967), Cavender (1978), Cross et al. (1986), Crossman and McAllister (1986), Fry (1973), Hensel (1980), Holcik et al. (1981), Illies (1978), Kolder (1966), Ladiges and Vogt (1979), Li (1984), Lindsey and McPhail (1986), MacCrimmon (1971), MacCrimmon and Marshall (1968), MacCrimmon and Campbell (1969), McPhail & Lindsey (1986), Minckley et al. (1986), Nelva et al. (1981), Nichols (1943), Penaz (1966), Poddubnyi (1979), Prawochensky and Kolder (1968), Spillmann (1961), Underhill (1986).

[d] Records for introduction not confirmed (Anonymous 1980 a, b).

[e] Originally present but became extinct; now re-introduced.

tions as well as input from local resource managers when possible. Salmonine abundance was assessed for two time periods: (1) historical, i.e., for the earliest records available for native species and prior to introduction for non-native species; and (2) recent, using the latest 10-yr average for catch plus escapement where available. In some cases only rough approximations could be made and in others little more than "educated guesses" could be attempted although evidence for direction of change between historical and recent periods was usually at hand. For non-anadromous salmonines in three major North American rivers (Table 11) it was possible to develop estimates of recent annual sportfish harvest and to apportion total catch between lake and river or stream habitat within each.

Three river systems — the Columbia, Fraser, and Skeena — clearly stand out as the major producers for salmonine fishes both in historic as well as recent times (Table 10). Another three were, and to a large extent still are, second-order producers (the Sacramento–San Joaquin, Yukon, and Amur) whereas the St. Lawrence has undergone major changes in salmonine production. Native species there have all declined greatly in production over the last 100 years but in recent decades the introduced Pacific salmon, mainly coho and chinook, have dominated annual yields though virtually all of this comes from the Laurentian Great Lakes rather than from the river itself.

Of the three major salmonid producers, the Fraser would seem to hold the edge historically as well as in recent times. Nevertheless, it would be useful to more closely compare abundance estimates with those for the Columbia and Skeena systems on a species by species basis (Table 11).

Three types of char (*S. malma* and *S. confluentus* are grouped into a single complex) occur in each system. With the addition of the U.S. catch of brook char (*S. fontinalis*) the total for the Columbia would surely be several hundred thousand, well above the hundred thousand estimate for the Fraser system. Only about a quarter of the brook char yield comes from rivers. Lake char (*S. namaycush*) occur in the U.S. portion of the Columbia by local introduction so catches probably are very small in comparison to indigenous

TABLE 10. Relative abundance[a] of salmonine fishes[b] in several large river basins of the world.[c]

River System	Time Period[d]	Brachymystax le	Hucho spp.	Salvelinus					Salmo					Oncorhynchus						Abundance "Score"[e]
				al	fo	m-c	na	le	sa	tr	cl	ga	ag	go	ke	ki	ne	ts	ma	
Sacramento-	H					4						3	2	1	1	1	1	6		19
San Joaquin	R				3	1				3		4	2	1	1	1	1	5		22
Columbia	H					4					5	6		1	5	6	6	6		39
	R				5	4	2			3	5	6	1	1	3	5	5	5		45
Fraser	H					4	4				5	6		6	6	6	7	5		49
	R				5	4	4				5	6		6	5	5	6	5		51
Skeena	H					4	4				4	5		6	5	5	6	5		44
	R				1	4	4				4	5		6	5	5	6	4		43
Yukon	H			4		2	4							1	6	4	1	5		27
	R			4		2	4				1	1		1	6	4	1	5		29
Mackenzie	H			3		2	5					1		1	2		1	1		16
	R			3	2	2	5			1	1	1		1	2		1	1		20
Churchill	H			1	1		5													7
	R			1	1		5					2								9
Nelson	H			1	3	2	4				2									12
	R			1	3	1	4			2	1	2	1							15
St. Lawrence	H			4	5		6		3											18
	R			3	4		5		1	5		5		5		5	2	5		41
Rhine	H			2	1				4	3										10
	R			1	1					1		4								7
Rhone	H			3						5										8
	R			2						4		3								9
Danube	H		4	3						6										13
	R		3	1	3					5		4								16
Amur	H	3	3			1		1						6	7			1	4	26
	R	3	3			1		1						6	6		1	1	4	26

[a] 1, recorded but numbers insignificant;
2, anadromous average annual runs < 1 000; resident populations isolated, average annual catches as for runs;
3, anadromous average annual runs < 10 000; resident populations scattered, average annual catches as for runs;
4, anadromous average annual runs < 100 000; resident populations common, average annual catches as for runs;
5, anadromous average annual runs < 1 000 000; resident populations widespread, average annual catches as for runs;
6, anadromous average annual runs < 10 000 000; resident populations widespread, average annual catches as for runs;
7, anadromous average annual runs > 10 000 000; resident populations widespread, average annual catches as for runs.

[b] le = *B. lenox*, al = *Salvelinus alpinus*, fo = *S. fontinalis*, m = *S. malma*, c = *S. confluentus*, na = *S. namaycush*, le = *S. leucomaenis*, sa = *Salmo salar*, tr = *S. trutta*, cl = *S. clarki*, ga = *S. gairdneri*, ag = *S. aguabonita*, go = *Oncorhynchus gorbuscha*, ke = *O. keta*, ki = *O. kisutch*, ne = *O. nerka*, ts = *O. tshawytscha*, ma = *O.masou*.

[c] Based in part on references in Table 8.1 as well as Allen (1977), Anon. (1973, 1973-1982, 1979, 1981), Argue et al. (1986), Aro and Shepard (1967), Bakkala (1970), Beacham (1984, a, b), Berg (1948), Billings (1983), Buklis (1981), Buklis and Barton (1984), Christie (1974), Emery (1981), Fraser et al. (1982), Fry (1977), Fulton (1970), Gaboury and Spence (1981), Gunsolus (1977), Hallock and Fry (1967), Healey (MS), Hensel (1980), Jungwirth (1978), Kasahara (1961), Korn (1977), Kwain (1982), Kwain and Lawrie (1981), Lake (1967, 1971), Lawrie and Rahrer (1972), Machidori and Kato (1984), Martell et al. (1984), Mauney and Geiger (1977), McCart and Beste (1979), McLeod and O'Neil (1983), Milligan et al. (1984, 1986), Moore and Olmstead (1985), Narver (1977), Netboy (1973), O'Neill and Lewynsky (1985), Pearse (1982), Percy (1975), Ricker and Manzer (1974), Sano (1967), Savvaitova and Maksimov (1980), Schulz (1985), Schulz and Piery (1982), Scott (1985), Scott and Lewynsky (1985), Shepard et al. (1985), Smith (1972), Starr et al. (1984), Stein et al. (1973), Stewart et al. (1981), Stone (1982), Van Hyning (1973), Vincent (1980), Wagner and Stauffer (1982), Weatherley and Lake (1967), Zarbock (1977).

[d] H = historical abundance; R = recent abundance.

[e] Sum of relative salmonine abundance indices.

TABLE 11. An approximate apportioning of the 1982 salmonid sportfish harvest estimates (thousands of fish) within three major drainage basins of British Columbia.[a]

Species	Columbia[b]			Fraser			Skeena		
	Lake	River	Total	Lake	River	Total	Lake	River	Total
Brook Char	75.0	26.3	101.3	89.3	15.0	104.3	—[d]	—[d]	—[d]
Lake Char				47.8		47.8	12.7		12.7
Dolly Varden[c]	40.0	20.0	60.0	25.3	8.1	33.4	0.9	41.1	42.0
Rainbow	1 239.1	172.0	1 411.1	1 346.5	197.9	1 544.4	147.6	13.5	161.1
Cutthroat	46.1	93.6	139.7	36.6	6.7	43.3	41.6	11.2	52.8
Kokanee	524.0		524.0	301.9		301.9	?		?
Coho					7.7	7.7		11.0	11.0
Chinook					7.4	7.4		?	?
Total	**1 924.2**	**311.9**	**2 236.1**	**1 847.4**	**242.8**	**2 090.2**	**202.8**	**76.8**	**279.6**
Percent		**13.9**			**11.6**			**27.5**	

[a] Based largely on recent regional management data of the B. C. Ministry of Environment, Fisheries Branch.
[b] Portion in British Columbia only.
[c] *Salvelinus malma* + *S. confluentus*.
[d] Insignificant numbers.

stocks of the Fraser and Skeena systems (about 48 000 and 13 000, respectively) but none is produced in riverine habitat. Populations of Dolly Varden and bull char show signs of depletion in the U.S. portion of the Columbia (Cavender 1978) but in the B.C. portion, catches are above those in the Skeena and nearly double those in the Fraser where about a quarter comes from river habitat.

Trout (*Salmo*) yields for the three systems come almost entirely from rainbow and cutthroat, with small additions from brown and golden trout only in the U.S. portion of the Columbia. With the addition of the U.S. steelhead catch alone (averaged about 181 000 between 1958–67; Fulton 1970), *S. gairdneri* catch for the Columbia would exceed 1.5 million annually, similar to that for the Fraser and an order of magnitude higher than that in the Skeena. Only about 10 % of the rainbow catch in any of the systems comes from rivers. Cutthroat catch clearly would be higher for the Columbia than for the Fraser or Skeena systems and the majority comes not from lakes but from river habitat, at least in the B.C. portion of the Columbia (Table 11).

Sportfish catches of salmon in the systems are dominated by "landlocked sockeye" (kokanee), all produced in lake rather than river habitat. Overall, for the B.C. portion of the Columbia and for the Fraser, river habitat only accounts for about 14 and 12 %, respectively, of the sportfish yield of salmonines whereas that in the Skeena is about 28 %.

All five species of anadromous eastern Pacific salmon occur in the three major river systems, but pink salmon are represented only sporadically by a few individuals (possibly strays) in the Columbia, both historically and recently. Fraser River pink salmon have long had sizeable spawning runs only on odd numbered years with catches from all sources historically in the order of 5 million. Over the recent 10-yr period (1973–82) catch in the Fraser management area plus Juan de Fuca, Georgia and Johnstone Straits probably has averaged just under 3 million annually with a stock size of well over 9 million on odd years (Pearse 1982). The Skeena has sizeable pink runs every year, although often smaller than the Fraser on odd years, so that catches have averaged about 572 000 over the 1973–82 period with stock sizes just under 2 million on odd years and just under 1 million on even years.

Chum salmon catches in the Columbia have declined sharply from an historical maximum in 1928 estimated at 708 000 to a recent 10-yr average of about 1 100 fish. Historical catches of Fraser chum considerably exceeded 1 million annually but have greatly decreased in recent years so that those for the Fraser and Juan de Fuca management areas have averaged about 140 000 with a stock size of about 776 000. A decline of similar proportion also has occurred for Skeena chum catches with historical levels of about 300 000 dropping to an average of 55 000 in the most recent decade.

Maximum historical catches of Columbia coho salmon (ca 990 000) occurred in the mid 1920s with a 1958–67 average of 352 000 from an estimated total run of 547 000 (Fulton 1970). Most recent catches (1973–82) have averaged 177 000 with a substantial portion from hatchery production. Fraser catches of coho reached maximum levels of about 1.2 million shortly after the turn of the century (Argue et al. 1986) but have declined to levels usually below 500 000 in recent years (1973–82 average of 303 000) from a stock size of 441 000 (Pearse 1982). Fraser et al. (1982) report a total return (terminal catch + escapement) of about 150 000 recently. Compared to the other two systems, the Skeena has always been a lower producer of coho with historic catches reaching 690 000, but dropping to catches averaging 62 000 in the recent decade from a stock size of about 131 000 (Pearse 1982).

Sockeye historic catches have exceeded a million fish in two of the systems (Columbia maximum in 1898 of about 1.3 million; Skeena maximum 1901–29 of 2.1 million) but in the late 19th and early 20th century, the Fraser had catches of 20 to 30 million sockeye in peak years (Netboy 1980) with an average of some 40 million per four year period from 1896 to 1915 (Ricker and Manzer 1974). The B.C. "South Coast" catches (predominantly Fraser River sockeye with a few hundred thousand from other minor stocks) have averaged about 5.4 million in the recent years (1973–82; Starr et al. 1984). Stock size averaged 4.5 million in the 1939–70 period (INPFC data) and has been somewhat higher (7.4 million) in the 1973–82 period (Starr et al. 1984) with 1982 being well over 14 million. The Fraser would seem to be the world's largest single river producer of sockeye, surpassed only by the total Bristol Bay stocks in Alaska which originate from several nearby, but separate, river systems. In comparison, Columbia River runs averaged only 151 000 in the 1946–74 period (Allen 1977) whereas those for the Skeena averaged about 1.2 million between 1951 and 1966 and more recently (1973–82), 2.4 million (Starr et al. 1984). The 1986 production of adult sockeye from the Fraser River was 15.8 million (Canada Dep. Fisheries and Oceans, 330-80-6th St., New Westminster, M. Farwell pers. comm.)

Finally, for chinook, the Columbia historically was the largest producer of the three systems with a maximum catch in 1883 probably exceeding 2 million fish (estimated from catch weight in Netboy 1973) whereas maxima estimated for the Fraser and Skeena in the early 1900s were 469 000 and 302 000 respectively. Recent catches (1973-82 averages) have been about 271 000, 104 000, and 27 000 for the Columbia, Fraser and Skeena respectively. Fulton (1970) gives an average for the total Columbia chinook run of 726 000 (1958 to 1967), slightly less than that of Korn (1977) for 1968–74 of 803 000. Total Fraser stocks have recently been estimated at 646 000 (Pearse 1982) and total return (terminal catch plus escapement) at about 200 000 (Fraser et al. 1982). The present Skeena stock size (41 000) is much lower than that of the other two systems.

In terms of current stock abundance for Pacific salmon, the Fraser, with a total of nearly 14 million, is clearly much higher than either the Skeena (4.2 million) or the Columbia (1.4 million). In terms of overall salmonine yield (Table 12), the Fraser, with current catches exceeding 12 million fish annually, is again well above the Columbia (2.7 million, neglecting the U.S. non-anadromous sport catch) or the Skeena (2.6 million). Only about a quarter of the Columbia River catch comes from species whose production is closely bound to riverine habitat, whereas that for the Fraser and Skeena is about 41 and 32 %, respectively (Table 12).

Salmonine Use of Tributary Rivers and Lakes

The sub-basins and mainstem of the Fraser River system are utilized by the five species of Pacific salmon in a very different and to some extent complementary manner (Fig. 13). Chum salmon are almost entirely confined to the lower Fraser, most entering the Harrison, with smaller runs to two minor sub-basins (Chilliwack and Pitt), as well as many small tributaries (Table 13). In addition, some chum salmon spawn in the mainstem Fraser between Chilliwack and Hope. Systematic surveys in the 1960s indicated an average of 77 000 chum may have utilized the lower mainstem areas (Palmer 1972). Recent estimates, based on restricted visual observations, show an average of 8 500 chum in the mainstem (Canada Dep. Fisheries and Oceans, 330-80-6th St., New Westminster, M. Farwell, pers. comm.).

Pink salmon, like chum, are mainly confined to the lower Fraser, but before the Hell's Gate blockage in the early 1900s as well as more recently with the advent of the fishways in the Fraser canyon, several hundred thousand now utilize lower portions of two middle reach sub-basins (Thompson and Bridge-Seton) with small numbers making their way upstream as far as the Quesnel River.

Coho salmon also heavily utilize tributaries of the lower Fraser and, like the pink, also enter the two lowermost sub-basins in the Fraser canyon (Fig. 13). However, unlike pink salmon, some coho move up tributaries almost to their furthest reaches.

Chinook salmon almost "cover the watershed" of the Fraser, entering in small numbers (Table 13) all major sub-basins and several minor ones, and extending up the mainstem almost to the uppermost reaches of the Fraser itself. In the middle and upper Fraser they tend not to pass through the large headwater lakes to upper tributaries, except in the South Thompson River (Adams–Shuswap Lake system).

Sockeye salmon, like the chinook, are widely spread through all Fraser sub-basins with accessible and generally

TABLE 12. A summary of recent salmonine catches (sport and/or commercial in thousands of fish; average annual where possible) in three large eastern Pacific coast rivers.[a]

Species	Columbia Total	Columbia River only	Fraser Total	Fraser River only	Skeena Total	Skeena River only
Brook Char	101	26	104	15	?	?
Lake Char	—[d]	—[d]	48	—[d]	13	—[d]
Dolly Varden[c]	60	20	33	8	42	41
Rainbow	1 411	172	1 544	198	161	14
Cutthroat	140	34	43	7	53	11
Kokanee	524	—[d]	302	—[d]	?	—[d]
Pink	—	—	3 500	3 500	574	574
Chum	1	1	341	341	55	55
Coho	177	177	380	380	96	96
Sockeye	—	—[d]	5 440	—[d]	1 541	—[d]
Chinook	271	271	578	578	19	19
Total	**2 685**	**701**	**12 313**	**5 027**	**2 554**	**810**
% River		**26.1**		**40.8**		**31.7**

[a] From data in Tables 10, 11 and associated background references.

[b] British Columbia portion only for char, trout, and kokanee.

[c] *Salvelinus malma* + *S. confluentus*.

[d] Not included because most of the inland water production occurs in lakes.

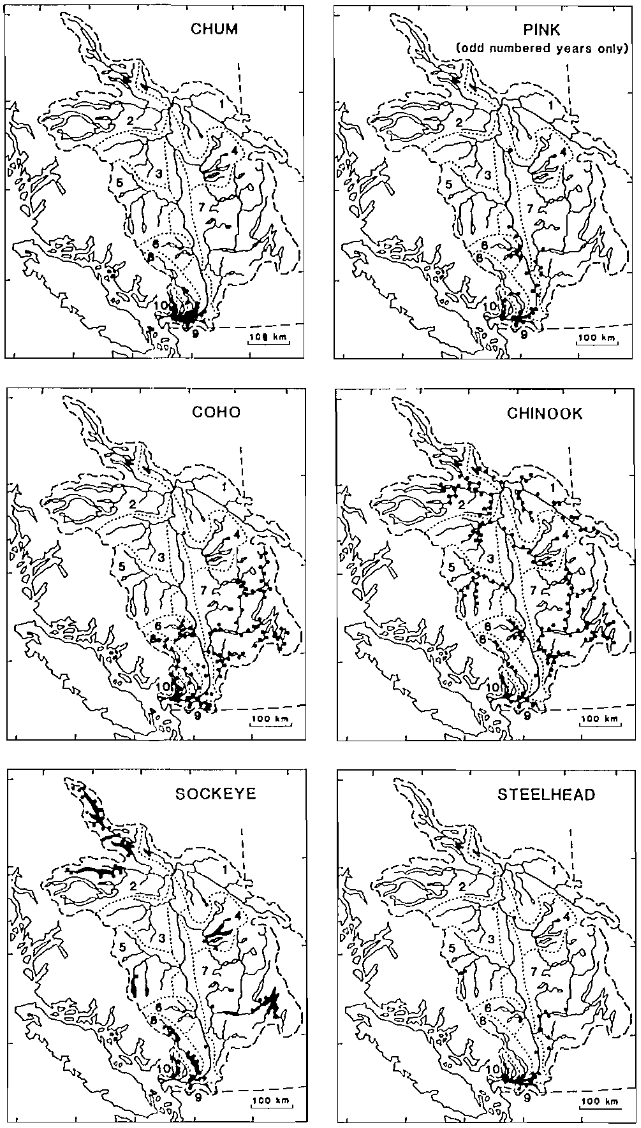

FIG. 13. The distribution of Pacific salmon and steelhead trout spawning areas[a] within 10 sub-basins and the mainstem Fraser River. Major rearing lakes for juvenile sockeye in black.
[a] in some cases where spawning areas are not well known symbols are placed near mouth of the sub-basin.

large rearing lakes (the Nechako, Quesnel, Chilcotin, Thompson, Harrison and Pitt river systems). Unlike chinook, sockeye salmon commonly extend their spawning grounds into smaller tributaries of their juvenile rearing lakes (Fig. 13) although there are some notable exceptions (e.g., Chilko Lake outlet spawning stock, as well as Harrison and Pitt river spawning stocks).

In addition to great spatial differences in use of the Fraser system by the five species of Pacific salmon, there are also important temporal differences in timing of both entry and spawning by the species and their various stocks. For example, chinook have spring, summer and autumn "runs" to different subsystems and all of the other species have early and late running stocks which may be separated by several months (Fraser et al. 1982). Chum salmon (Anderson and Beacham 1983), coho salmon (Fraser et al. 1982) and sockeye salmon (Foerster 1968) stocks of the Fraser River also show marked seasonal differentiation in migration timing. The picture that emerges is one of a complex, highly diversified watershed with many large sub-basins, most of which are heavily used by the salmon species and their stocks but to different extents and at different times.

Added to this complexity, there are two species of anadromous *Salmo* — the steelhead (*S. gairdneri*) and the "sea-run" cutthroat (*S. clarki*) — as well as anadromous Dolly Varden and bull trout (*Salvelinus malma* and *S. confluentus*) which utilize Fraser River tributaries. Cutthroat and Dolly Varden are for the most part confined to the mainstem and tributaries of the lower Fraser, but steelhead move up the middle reaches and into the Thompson and Chilcotin sub-basins with a very few ascending above the West Road sub-basin (Table 13).

In recent years an average of over 5 million salmonine fishes migrated into the Fraser River system annually (Table 13). In the odd-numbered years the greatest numbers spawn in the lower mainstem reaches (mostly pink salmon), but in many even-numbered years the Thompson sub-basin has the highest salmonine spawner densities. The Harrison, on average, receives over 13 % of the anadromous salmonine escapement annually, and four other sub-basins each receive over 5 % (Nechako, Quesnel, Chilcotin, and Bridge-Seton).

Most lower Fraser tributaries and lakes maintain resident populations of rainbow trout, cutthroat trout, native and introduced char as well as non-anadromous sockeye salmon (kokanee) in many of the lakes. With the absence of cutthroat trout and the addition of lake char (*Salvelinus namaycush*) in most large lakes of the middle and upper sub-basins, a similar pattern is repeated for interior parts of the Fraser watershed.

Some 43 of the 100 lakes surveyed over thirty years ago (Northcote and Larkin 1956) to consider factors controlling productivity and typology of British Columbia inland waters lie in the Fraser watershed. Additional material on several of the more important lakes is reviewed by Northcote and Larkin (1963), Ward (1966) and St. John et al. (1976). Because of the importance of lake conditions to juvenile sockeye salmon production there has been a long series of limnological studies on sockeye lakes of the Fraser system (see for example Foerster 1925, Ricker 1937a,b, Ward 1957, Goodlad et al. 1974, Stockner and Shortreed 1983). Despite the proximity of hard, nutrient-poor, granitic rocks along the western flank of the Fraser watershed and of metamorphic schists and gneisses of the Columbia Mountains on its southeastern limits (Fig. 1), most of the important sockeye producing lakes lie largely in softer stratified sedimentary or volcanic formations where nutrient supply might be expected to be higher than in coastal waters. Using more elegant technology but basically the same approach as Northcote and Larkin (1956, 1963) to recognize limnological regions of differing lake productivity, Stockner and Shortreed (1983) found that 19 lakes in the Fraser watershed can be classified into 3 groups on the basis of several chemical and biological "production indices". Lakes in their two zones of higher productivity are situated in the central and northern interior. In contrast, the watersheds of many of the lakes in their zone of low productivity lie mostly in hard granitic formations of the Coastal Mountains. Stockner and Shortreed (1983) mistakenly state that Northcote and Larkin (1956, 1963) consider the length of the growing season to

TABLE 13. A summary of recent average annual salmon escapements and estimated steelhead escapement (thousands) in major drainage sub-basins and the mainstem Fraser River.[a]

Sub-Basin	Chum[b]	Pink[c]	Coho[b]	Chinook[b]	Sockeye[d]	Steelhead[e]	Total[f]	%
1. Upper Fraser	0	0	0	16.1	8.4	0	24.5	0.5
2. Nechako	0	0	0	2.7	258.4	0.1	261.2	5.1
3. West Road	0	0	0	3.2	0	1.4	4.6	0.1
4. Quesnel	0	0.4	0.1	2.3	269.8	<0.1	272.4	5.4
5. Chilcotin	0	0	0	6.3	285.1	0.8	292.2	5.8
6. Bridge-Seton	0	467.3	1.4	0.5	18.2	0.3	254.0	5.0
7. Thompson	0	624.1	13.2	26.2	741.7	6.6	1 099.7	21.7
8. Harrison	295.2	304.7	19.0	22.5	171.7	1.0	661.7	13.1
9. Chilliwack	92.2	97.7	10.1	0.2	11.0	9.4	171.7	3.4
10. Pitt	1.9	0	5.5	0.3	19.4	3.0	30.1	0.6
11. Mainstem Minor Trib's.								
a. Lower	112.9	32.2	14.3	<0.1	<0.1	1.0	144.3	2.8
b. Middle	0.2	73.7	1.8	1.2	1.7	0.8	42.5	0.8
12. Mainstem								
a. Lower	8.5	3 603.0	0	0	0	1.2	1 811.2	35.7
b. Middle	0	0	0	0	0	0	0	0
Total[f]	**510.9**	**2 601.6**	**65.1**	**81.5**	**1 785.4**	**25.6**	**5 070.1**	
%	**10.1**	**51.3**	**1.3**	**1.6**	**35.2**	**0.5**		**100.0**

[a] Salmon data from Canada Dep. Fisheries and Oceans, New Westminster; does not include hatchery counts (11.6 thousand coho); steelhead data from Billings (1982, '83, '84, '86) and Ford (1982) used as follows: average total catches were scaled by one of four factors depending on average annual angling pressure (< 100 days fished = 0.05; 100–500 = 0.1; 501–1000 = 0.2; 1001–10 000 = 0.3; 10 001–15 000 = 0.4; > 15 000 = 0.5, based in part on Pautzke and Meigs 1940, Hallock et al. 1961, Peterson and Lyons 1968) to make estimates of available adults from which the average catch was subtracted to estimate average escapement.

[b] 1981-85.

[c] 1981-85, odd numbered years only.

[d] 1978-85 to include two cycles with dominant years.

[e] Averaged for five angling seasons (1980-81 to 1984-85).

[f] Totals adjusted by halving pink escapement to account for odd year runs only.

be one of the most important factors in controlling productivity levels of British Columbia lakes. We concluded our 1956 paper with the statement that "Considering lakes throughout the province, edaphic factors as measured by total dissolved solid content of the water appear to be most important in determining the general level of productivity". Their more recent work re-emphasizes that view.

Salmonine Management

The management of Pacific salmon populations conforms to a common pattern along the whole of the northwest coast of North America: (1) the catch of each stock is regulated so as to achieve an escapement that will maximize production; (2) there are strong efforts to protect salmon habitat from encroachment of other resource uses; and (3) measures are taken to enhance natural production by a variety of means (Larkin 1970). The Fraser River provides a typical example of the complexity of applying these measures in a large natural system in the circumstances of intensive utilization of both the fish resources and other natural resources.

The regulation of the catch of Fraser salmon involves a number of simultaneous considerations. In accordance with treaty arrangements with the United States, the catch of Fraser River fish is shared. The details are complex. The essential principles are a recognition of historic patterns of sharing and an acknowledgement that any increases in production from enhancement measures belong to Canada. Both countries have commercial and recreational fishermen, and in both countries the commercial fishermen are subdivided by the type of gear that is used: troll, seine or gill net. Native food fisheries that date from prehistory and that are maintained to the present day are a current source of controversy that is complicated by native land claims unresolved by treaty at the time British Columbia joined confederation and which remain unresolved today. Allocation of the catch by country and fishing sector thus presents some difficult social and political problems.

Even without these complications the catch regulation for Fraser River salmon stocks is inherently difficult. Each of the five species comprises a large number of stocks associated with various tributaries. Sockeye stocks for example, are each associated with a particular rearing lake (Stuart, Chilko, Quesnel, Shuswap, etc.) and within a rearing lake may be associated with particular spawning tributaries. The timing of the freshwater migration of the adult fish is broadly adapted to the circumstances of the rearing environment so that the various stocks are not all fished at the same time. Nevertheless, there is enough overlap that it is difficult to regulate the catch of each stock separately. In general, the stocks which use the lakes at higher elevations further inland proceed through the fishery earlier than those which use coastal lakes at lower elevations; those which use more northerly tributaries are earlier than those in the south. The fishery is managed on a day-to-day basis with estimation of the proportions of each stock in the catch. While the regulation is technically sophisticated, the harvest is only as precisely controlled as circumstances permit.

Regulation of the harvest of sockeye salmon is echoed in that of the other species, each of which have a large number of component stocks with characteristic timing in the fishery. There are thus not only the problems of regulating the catch of each stock when several stocks of a species are caught at the same time, but also the problem that several stocks of different species may be taken at the same time. Because sockeye and pink salmon are much the most abundant, the rates at which they are harvested strongly influence the rates at which all species are taken, for it is difficult to fish in such a way as to exclude the other species of Pacific salmon. (Those stocks of steelhead which migrate during the salmon season are also taken in the same gear.)

A major feature of the fishery for sockeye and pink salmon is the strongly cyclical nature of the populations. In the Fraser, pink salmon have a virtually invariable two year life span and are overwhelmingly more abundant on the odd numbered years, the even years having only a very few thousands compared to millions in the odd years. Some sockeye populations have a characteristic 4-yr cycle of abundance which has been called "dominance", explanations for which were first systematically considered by Ricker (1950) and which evidently are related to the predominant age of maturity of 4-yr.

Prior to 1913 the Fraser River sockeye were far more abundant ("dominant") on the 1909, 1913 cycle. The large upstream populations (Quesnel, Stuart, Adams) were all apparently dominant on the same year, which led Ricker (1950) to suggest that predation in the main stem of the river, the estuary and perhaps at sea might be responsible for synchronizing cyclical behavior. The recovery of the Adams River sockeye stock began in 1922 after the removal of a logging dam and the stock has since been dominant on the 1922, 1926, ... 1986 cycle, producing a total of from 5 to 15 million on the dominant year, 1 to 5 million in the following (subdominant) year and a few thousands of fish in the two "off" years. Ward and Larkin (1964) attributed this pattern of abundance to the interaction of sockeye and predator populations which led to strongly depensatory mortalities in the off years. The fishery may also have the effect of being depensatory in the odd numbered years when the harvesting of pink salmon may result in taking sufficient sockeye to keep their abundance down. In recent years, the various large stocks of sockeye from upstream lakes have not been dominant on the same year, perhaps reflecting in part their differential susceptibility to harvest in conjunction with pink salmon. Regardless of its causes, dominance is a major phenomenon of Fraser River salmon management.

Coho are predominantly three years old at maturity, chum are roughly 70% 4-yrs old at spawning (Beacham 1984a) and chinook have an average age at maturity of slightly over four (Healey 1982) and there are no persistent cyclical fluctuations. Fluctuations in abundance are exacerbated by depensatory mortalities in all of the fisheries and pose serious problems of management, especially for chinook salmon.

The sport fisheries for salmonines in the Fraser River and its tributaries are as much driven by demand as by supply. Although lip service may be given to the notion of maximum sustained yield, regulations are essentially designed to enable recovery of stocks that are threatened, to distribute the catch among the fishermen, or to sustain the ethics of sportsmanship. Because most lakes above 1000 m are not accessible to fish from downstream, a large number of lakes contain only those species that have been introduced, by design or by accident. Many contain only *S. gairdneri* and, lacking suitable spawning facilities, require annual stocking.

For both salmon and trout there have been continuing efforts by both levels of government to maintain the quality of habitat in the face of increasingly greater use of the various resources of the Fraser basin. Forestry practices, mining activities, gravel removals, irrigation diversions, hydroelectric developments and a variety of sources of pollution have from time to time made inroads on Fraser River salmonine production. The details would require a long exposition. It may suffice to indicate that there is a current policy of "no net loss" of salmonine habitat and there have been substantial efforts over the course of the past century to take measures to redress harmful impacts. While it is easier to make policies at federal and provincial offices than to carry them out where the salmon spawn, there is considerable optimism that the attrition of habitat has been slowed to a virtual standstill.

Over the past century there has also been a sustained effort to enhance the natural production of salmonines by artificial methods. Initially, attention focussed on the crafts of fish hatcheries coupled with attempts to establish populations where they did not naturally occur. For rainbow trout these techniques were successful for stocking of lakes that contained no fish ("barren lakes") and for annual stocking of lakes with no natural spawning facilities. Less success attended attempts to establish non-native species such as brook char. The record of hatcheries for sockeye salmon was put in question by the study of Foerster (1938) on Cultus Lake and shortly thereafter the federal government discontinued its hatchery program, assigning all of the facilities to the provincial government for the purposes of trout culture.

By the early 1950s the potential impacts of hydroelectric developments and the successes of some experiences in the United States combined to renew interest in hatcheries and other methods of enhancing salmon populations. The International Pacific Salmon Fisheries Commission, with responsibility for Fraser sockeye dating from the late 1930s and for Fraser pink salmon after the early 1950s, engaged in a variety of enhancement activities including the construction of spawning channels for sockeye salmon at Weaver Creek (Harrison River) and Gates Creek (Birkenhead River), and for pink salmon at Seton Creek near Lillooet. The rebuilding of the once large sockeye populations of Quesnel Lake by a combination of regulating the catch and enhancement measures on the Horsefly drainage has been a major success. Attempts to re-establish the Upper Adams River stock which uses Adams Lake for rearing have only recently shown encouraging signs of population increase above trivial levels.

During the 1970s and 1980s there have been major salmonid enhancement activities in a joint federal–provincial program but relatively little attention was given to the Fraser because it was perceived that if Canada paid all the costs the United States would get half the benefits, and if the United States paid half the costs it would reinforce their claim to half the allowable catch. With the treaty arrangements completed in 1984, Canada will provide all of the costs and reap all of the benefits of enhancement (assuming they can be quantified).

The enhancement of salmonine resources includes a variety of techniques ranging from provision of fishways at difficult points of passage, spawning channels that are in essence designed streams, egg boxes (pink and chum), to hatchery operations of varying duration for chinook and for a full year for coho. Fertilization of lakes of low productivity is also being attempted experimentally. It is to be expected that all of these techniques will be intensively applied to the Fraser system in the coming decade. Particular attention will be given to rebuilding of chinook and chum salmon stocks which have been depleted by rates of harvesting in excess of that which the stocks can sustain on a continuing basis.

The greatest area of concern for the future of Fraser River salmon is the regulation of the fishery. The consequences of excessive rates of harvesting which were and are in part responsible for the depressed status of some stocks of some species are fully appreciated by management authorities. It remains to be seen whether the social and economic pressures of the fisheries can be moderated in the interests of conservation. There will be need, of course, for continued vigilance in protecting the environment and for enhancement measures to rectify past mistakes to compensate for contemporary inadequacies of management, but with perseverance, the salmonine abundance will be maintained at least at present levels and may well be returned to historic levels.

Dams and Diversions

The rugged terrain of British Columbia and the moderate to heavy precipitation combine to make most of the major rivers attractive for large hydroelectric developments. The Fraser is no exception. In the lower reaches of the river, two hydroelectric dams were built on the Stave River and one on the South Alouette River prior to World War II, and another was built on the Coquitlam river for storage. Subsequently, there have been a variety of schemes for damming major tributaries and the main stem of the river.

In the early 1950s, the Aluminum Company of Canada constructed the Kenney dam on the Nechako river, reversing the flow of the drainage through a tunnel under the Coast Mountains to a powerhouse on the Kemano River which supplied power to an aluminum smelter at Kitimat on the coast. This diversion had the beneficial effect of lessening the likelihood of flooding in the lower reaches of the Fraser (there had been a serious flood in 1948) but at the expense of inundating the forest surrounding the Great Circle chain of lakes that bounded Tweedsmuir Park and contributing to higher water temperatures in the residual flow of the Nechako downstream as far as Prince George, with attendant harmful effects on several stocks of sockeye and chinook salmon. Recently, it was proposed that a second phase of this project should be implemented that would (among other effects on the Skeena drainage) exacerbate the harmful effects on the Nechako (Jackson 1984).

The company has now reached agreement with Fisheries and Oceans Canada for a modified version of the second phase development. Under the terms of the agreement minimum flows are to be provided to the Nechako, provision is to be made for drawing cooling water from depths of the reservoir, a scheme for monitoring impacts on fish stocks will be implemented, and mitigation measures will be taken if warranted.

Another major development proposal was the diversion of the McGregor River (a Fraser tributary upstream of Prince George) into the Parsnip River (Peace–Mackenzie River system). The project featured dams at each end of a reservoir, at the downstream end to block the McGregor and at the upstream end to prevent migration of fish from the Peace drainage into the Fraser system. The project has been shelved, in part because of the risk of inadvertent introduction of fish and fish parasites into the Fraser drainage (Seagel and Pugh 1981; Arai and Mudry 1983). There would also have been significant effects downstream from the lowering of water levels and increases in temperature (Yung 1979; McLeod 1979).

The prospects of introduction of fish and parasites as a consequence of proposed major drainage diversions in the region were comprehensively considered by Lindsey (1957) and included consideration of the possible effects of diversion of the Finlay and Parsnip rivers (Peace drainage) into the Fraser, the Skeena into the Fraser by a dam on Babine Lake, the Chilko River (Fraser) into the Southgate or Homathko rivers (Coastal drainages) and the diversion of the Columbia into the Fraser by a dam at Mica Creek. After consideration of a variety of possibilities for development of the Fraser to reduce risks of damaging floods and to minimize impacts on salmon, a joint advisory board to the federal and provincial governments recommended in 1963 what was called "System E". In this scheme there were nine projects, including the McGregor, and a dam on the mainstem of the Fraser upstream of the confluence with the McGregor (Anonymous 1963). In various degrees all of these schemes have had an element of fantasy, the Columbia diversion being a bargaining ploy in difficult negotiating with the United States. Fortunately again, none of these schemes has come to pass.

The Columbia diversion would have involved the construction of a series of dams in the Fraser canyon for which the problems of fish passage were considered insurmountable even at an expenditure of several hundred million dollars. The problems of fish passage at proposed high dams of the Fraser and the impacts of dams and diversions were sketched by Andrew and Geen (1960) and more generally by Dussart et al. (1972). Upstream migrants are on a relatively inflexible time and energy regime that cannot tolerate long delays. It is relatively easy, though prohibitively expensive, to design facilities that could accommodate the numbers of fish involved, but it is quite another matter to devise techniques for enticing the fish to make full and prompt use of the facilities. Downstream migrants pose similar problems of quick passage because they must be guided safely downstream, avoiding the spillway or turbines. Much of the same sorts of problems were posed by a proposal to build a very high dam at Moran, a short distance upstream of the confluence of the Thompson and Fraser rivers. The potential effects of this development were reviewed by Geen (1975) and included a detailed assessment of downstream effects which had previously not been given adequate consideration. The Moran dam proposal is resurrected from time to time, but with decreasing vigor. The essay of Haig-Brown (1972) only needs dusting off to provide an eloquent and effective rebuttal.

Aside from the Nechako dam the only developments on the Fraser in the past 40 years have been relatively small in scale and impact. The diversion of the Bridge River to the Seton–Anderson system, tributary to the Fraser near Lillooet, and a dam on Wahleach Lake diverting water to Jones Creek near Hope, were both provided with artificial spawning channels for pink salmon and neither have posed serious problems of fish migration. The effects of the Seton diversion on the limnology of Seton Lake were considered by Geen and Andrew (1961).

It is an interesting footnote of history that the two very large sockeye producers of the Fraser today were both decimated by small dams early in the development of the province. The Quesnel River run was almost wiped out by a dam constructed to facilitate placer mining operations and it was only through the strenuous efforts of the then Fisheries Commissioner, John Pees Babcock, that the run was salvaged. A logging dam on the Adams River decimated the sockeye stocks of both the upper and lower Adams River. The lower river run is now large and famous and there are signs that the upper river run may at long last recover too.

Throughout the Fraser there have been many local diversions or obstructions which from time to time have had unfavorable effects on salmon and trout. Most of these effects have been redressed, and with current levels of surveillance there is much less likelihood of a slow attrition of productive potential from a multitude of minor impacts. The most famous of these obstructions was at Hell's Gate where the dumping of rock cut material from Canadian National railway construction resulted in virtually complete blockage of early and mid season stocks in the big run year of 1913.

The vertical profile of the Fraser canyon at Hell's Gate is hourglass in shape so that at high and lower water levels salmon, which migrate near the surface at the river margins, can get through. At the intermediate levels which are characteristic at the time of migration for early and mid-season stocks, passage is extremely difficult. (The Adams River run was not severely affected by the blockage as it is a very late season run.) For several years following the blockage, attempts were made to ease fish passage by rock removals, but is was not until after the signing of the treaty between the United States and Canada in 1937 that work began on fishways. Their completion, coupled with close regulation of the fishery, was responsible for the recovery in whole or in part of several of the upstream stocks of sockeye. Pink salmon had virtually disappeared from the Fraser upstream of Hell's Gate, but since the construction of the fishways they have recolonized the Thompson, the mainstem as far upstream as Quesnel and tributaries such as Seton Creek, recovering most of the range. It is appropriate in concluding this brief summary of dams and diversions to note that the recent proposal to doubletrack the Canadian National railway through the canyon was very carefully reviewed by a team of engineers and fisheries specialists and resulted in the development of a plan that would probably enhance rather than obstruct fish passage. Unfortunately, the plan was developed without consideration of native Indian claims for traditional fishing privileges and implementation has been delayed pending legal proceedings (Thompson 1986).

Waterfowl, Wildlife, and Recreational Values

As might be anticipated from its size, the Fraser River provides substantial habitat for a wide range of aquatic birds and mammals (see Taylor 1974; Halladay and Harris 1972; Drent et al. 1971 for details), and the terrain through which the river passes offers significant recreational opportunities.

For many people, the fish and wildlife of the Fraser are sufficient recreational attractions; others are more taken with the scenery as the river passes from wooded mountain slopes at its origin in the Rocky Mountain trench, through the interior parklands and the spectacular Fraser Canyon to the lower Mainland. Still others enjoy the experience of river rafting the dangerous passages of the canyon or kayaking the more turbulent tributaries. It is for these reasons that from time to time there have been proposals that the river and adjacent lands should be managed as a recreational corridor, a strip in which the various resource uses would be undertaken with particular awareness of recreational values. This is not an easy undertaking because the river valley downstream of Lytton is also a natural transportation corridor, accommodating two transcontinental railway lines, oil and gas pipelines, the Trans Canada highway and a large hydroelectric transmission line. Both railway lines are gradually adding trackage to eventually achieve double tracking and the highway is periodically enlarged. With such intensive use for transportation it is evident that there must be some infringement of recreational potentials.

Much of the recreational value of the Fraser is centred on its salmonid resources, not just for their attraction as sport fish, but because the spectacle of their annual migration is part of the natural heritage of the region. A survey of residents (Meyer 1978) led to the estimate that for residents downstream of Hope the salmon and steelhead of the Fraser had an annual value of $74 million for recreation and $92 million for preservation of aesthetic values. For residents upstream, comparable figures were $18 and $22 million. These estimates may seem large, but when more than 100 000 visitors visit the Adams River in the quadrennial "Salute to the Sockeye" there is little doubt that salmon play a major role in the provincial culture.

An Overall Assessment of Fraser Salmonine Production

Having shown that the Fraser River was and still is one of the largest producers of salmonine fishes in the world, and having reviewed some of its more important physical and biological characteristics, we now must attempt an assessment of the major functional features which lead to its first order status. These may be conveniently grouped into four categories: (1) physical features, (2) water quality, (3) salmonine diversity, and (4) human interactions.

Physical Features

Although not one of the really large rivers of the world (see Welcomme 1985, table 1.7), whether ranked by mean annual discharge or by length, the Fraser is well within the top 30 systems. For some salmonine species such as chinook (Healey MS) there is a strong positive correlation between river discharge and the size of the spawning population, but for others no such relationship exists. Enormous sockeye populations are produced from several rather small rivers emptying into Bristol Bay, Alaska and one only moderate sized river in Kamchatka may host spawning populations of pink salmon exceeding 10 million on some years (Berg 1948). Overall salmonine production does not seem to be necessarily correlated with river size, though being large does permit sufficient sub-basin diversity to accommodate a wide variety of salmonine species and stocks. The latter point seems to be nicely illustrated by the Fraser system with at least 10 sizeable sub-basins, all with a wide range of salmonine species and stocks, as well as a large number of smaller tributaries some of which support consequential runs of salmon or trout. Furthermore, parts of the lower mainstem river itself provide important spawning grounds for at least one species, the pink salmon.

Four other physical features of the Fraser are linked to its high salmonine productivity. First, and of great significance to its sockeye production, is the complex network of large lakes accessible to adult upstream migrants, well distributed throughout the middle and upper reaches of 8 of the 10 major sub-basins (Fig. 13). The key importance of this feature is clearly shown by the uppermost sub-basin, with only one small lake (Bowron) which supports the smallest population of all sockeye producing sub-basins, and the West Road sub-basin, whose headwater rearing lakes are inaccessible to upstream adult migrants and produces no sockeye (Table 13). In addition to provision of juvenile rearing habitat for sockeye salmon, large headwater lakes may serve as long-term hydraulic balances on the downstream system, favouring successful spawning, rearing and migratory conditions for many other species of salmonine fishes.

Secondly, as a result of its relatively high discharge, even in the middle and upper reaches, combined with its moderately high turbidity, the mainstem Fraser serves as a very efficient migration route for both adult and juvenile salmonines. Although there are and probably have long been a few points of difficult passage for adults in the central canyon, because of the low profile over some 1 200 km of its length (Fig. 4), the Fraser provides adult salmonines access to most major sub-basins and their tributaries. In addition, the young downstream migrants may enjoy relatively safe descent to the river mouth in a medium where in-river, estuarine and near-coastal predation could be reduced considerably by moderate turbidity.

Thirdly, for at least two if not three salmonines (chinook, chum, and some sockeye stocks) the well developed estuarine tidal channels provide a rich productive habitat conducive to rapid juvenile growth and subsequent high survival at sea.

Finally, it should not be overlooked that the Fraser discharges its juvenile salmonine load into one of the more productive ocean rearing habitats in the northeastern Pacific (Parsons et al. 1970), further enhanced by a complex of coastal islands and inlets.

Water Quality

Despite the abuse of the recent and various activities of European man, in general the water of the entire Fraser River system retains remarkably good quality. In large part this is a fortuitous outcome of the high initial water quality, the stabilizing effects of large tributary lakes and the high volume of discharge along much of its length. To be sure there are some problems but for the most part these still remain minor and localized. This should not lead to complacency. Natural endowments and luck have been major contributors to good water quality and the potential for a catastrophe is increasing.

Because of relatively high buffering capacity, the possibility of any significant change in pH resulting from acid fallout seems remote for most of the mainstem river and many of its tributaries. Thus the Fraser system should escape for the time being the ravages of acidification which have decimated or eliminated salmonine fish production in some eastern North American and European rivers. The westerly airflow across the expanse of the Pacific must limit the possibilities of high acid fallout onto the watershed in general. Nevertheless, there have been highly acidic rains reported in parts of the lower Fraser Valley where tributary waters are not well buffered.

Many of the large lakes within upper reaches of the major drainage sub-basins lie in geological formations where the added effects of continental climate are conducive to moderate nutrient levels and low flushing rates. This does not mean that their present productivity could not be enhanced by careful and appropriate lake fertilization techniques. For some of these lakes, high glacial flour turbidity combined with low nutrient levels and sub-optimal temperature conditions must severely restrict production for several salmonine species.

Salmonine Diversity

Apart from the fact that the Fraser River has one of the highest diversities of native salmonine fishes of any large river supporting salmonines (Table 9), most of the species are further subdivided into discrete stocks which utilize different portions of particular sub-basins at highly predictable times of the year. Thus we see many examples of early or late, spring or summer or autumn or even winter "runs" to certain tributaries. Also there are many differences in lower, middle and upper reach runs of several species of salmon as well as steelhead trout. Meristic, protein isozyme, behavioral and other characteristic differences of these stocks show that they have a strong genetic basis (Beacham and Murray 1985, 1986; Taylor and Larkin 1986; Wehrhahn and Powell 1987; Taylor and McPhail 1985a,b; Brannon 1972; Tsuyuki and Williscroft 1977). Thus there would seem to be much genetic "fine-tuning" developed in stocks of each salmonine species to most effectively "exploit" sub-basin diversity and potential so as to maximize their reproductive success. Of course this feature of salmonine evolutionary biology is not unique to the Fraser system but it does seem to be developed to a very high degree, probably as a result of the diversity provided by the system and the large number of salmonine fishes which now utilize it.

Although there is high salmonine diversity in the Fraser system, it must be noted that at least in recent years as well as probably in the historical past, by far the greater part of the river's salmonine production came from only two species — pink and sockeye salmon. On a several year average these species now account for about 87 % of the total catch of anadromous species (Table 12) and about 86 % of the total escapement (Table 13). On odd-numbered years with the high contribution of pink salmon the percentages would be substantially higher. Runs of the other three salmon have recently been considerably below historic or even mid 1900 levels, but then as now the dominance of pink and sockeye in the system was undisputed. For most sockeye stocks production up to the seaward migrant stage is heavily dependent on rearing lakes and their productivity. Thus to that extent they may properly be considered a river system "product." Not so for the pink salmon. No one would deny their dependence upon suitable river habitat and conditions, but to a major degree pink salmon production (in terms of biomass) comes essentially from the sea rather than the river system.

Human Interactions

Native people of the Fraser probably began to use its rich salmonine resources several thousand years ago as is suggested by archaeological studies in the lower end of the Fraser Canyon (Borden 1968), but more direct evidence is needed to establish timing (D. Pokotylo, Department of Anthropology, Univ. Brit. Col., pers. comm.). The dependence of native Indians on salmon was substantial, but whether their harvest had a significant impact on abundance is arguable. It would be expected that the catch would tend to be a depensatory mortality (Larkin and McDonald 1968) removing a greater proportion in years of low abundance. A recent study has suggested that the catch may have been much larger than is usually assumed (A.W. Argue, 1751 Barrie Rd., Victoria, B.C., pers. comm.) but there is no firm evidence that aboriginal fisheries were a major factor in limiting abundance or distribution.

Commercial exploitation of Fraser River salmonines by European man started in 1829 when some 15 000 sockeye were salted and exported in barrels. From this modest beginning the fishery expanded rapidly in the late 19th and early 20th century, reaching a maximum catch in 1913 of over 30 million fish, most of which were caught by gill nets in the lower reaches and near the mouth of the river. At the close of the 19th century, nearly full use of the stocks was reached (Larkin and Ricker 1964), and catches from some cycles (the "1903" and "1904") declined to less than 25 % of their former maximum shortly more than a decade later. Nevertheless, the Fraser was at this time the largest producer of sockeye salmon in the world, relying heavily upon catches from the dominant 1901 cycle years.

The Fraser River, in sharp contrast to that of its nearest neighbour large river, the Columbia, has had no dams placed along its 1375 km long mainstem. Perhaps principally for this reason, the Fraser still enjoys its predominant position in the list of salmonine producing rivers of the world. The fact that an unobstructed migration passage for salmonines has been maintained in the mainstem river in a province at times "hell bent" on industrial development is highly significant. Other forms of mainstem industrial or urban development, apart from that at Prince George and Quesnel, have largely taken place near the mouth of the river where sheer volume provides some buffering from pollutant discharge.

Many of the highly productive backwaters and marshes that once connected directly to the lower reaches of the river over the last century have been cut off by extensive agricultural draining, dyking and flood-control measures. Despite heavy use of the North Arm of the Fraser estuary for log booming (Levy et al. 1982) coupled with ever-expanding urban development on the river delta, a surprisingly large area of estuarine marsh still remains in relatively undisturbed condition and provides temporary residence as well as feeding areas for four species of young salmon (Levy and Northcote 1982: Levings 1982).

Though not without its problems and minor shortcomings, the management of the various salmonine species and stocks of the Fraser system has been remarkably successful over the past four decades since intensive efforts began. Fishways have allowed partial recovery of many stocks to the middle river sub-basins, and spawning channels such as those at Weaver Creek on the Harrison subbasin, along with additional measures, have re-established runs that were heavily depleted by harmful effects of logging. These and other enhancement techniques seem reasonably sure to further restore salmonine runs of the Fraser to historic levels or more over the next few decades. Perhaps one of the most exciting possibilities for enhancing Fraser River salmonine production in a major way would be the development of an even-year pink run (Williams 1976) but disease problems in rearing have thwarted recent efforts.

In conclusion, we have documentated the case for the Fraser system being one of the truly great salmonine producers of the world and have offered several lines of explanation. The mainstem river, though critically important throughout the year as a migration channel for adults and young as well as for spawning and egg to fry rearing of two species during autumn and winter, is not a major source of production except in its lowermost reaches in the estuary tidal channels. Most of the production occurs in large headwater lakes, in clear tributary streams, or in the ocean. The reasons for low production within most of the mainstem include: (1) high level and seasonal change in discharge; (2) high turbidity even when clearest in winter; (3) relatively cool thermal regime; (4) only moderate levels of primary nutrients; (5) few meanders, backwaters or side-channels along much of its length; and (6) low primary and only moderate levels of secondary production. In these respects the Fraser is probably not atypical of many large rivers such as the Skeena, Nass, Stikine and Yukon along the western coast of North America, all of which produce major salmonine runs albeit in total numbers well below those of the Fraser. Salmonine fishes with their characteristic diversity and plasticity surely have "seized upon" one of the most favourable riverine systems to demonstrate their remarkable productivity.

It may well be that other river systems of the North Pacific will some day surpass the Fraser as a river for salmonines. The combination of natural advantages, moderate and reasonably controlled development and moderately successful management could be eroded while other systems maintain or surpass their current production. Meanwhile, the pre-eminence of the Fraser should be valued and preserved.

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References

ALBRIGHT, L. J. 1977. Heterotrophic bacterial dynamics in the lower Fraser River, its estuary and Georgia Strait, British Columbia, Canada. Mar. Biol. 39: 203–211.

ALBRIGHT, L.J., T.G. NORTHCOTE, P.C. OLOFFS, AND S.Y. SZETO. 1975. Chlorinated hydrocarbon residues in fish, crabs, and shellfish of the lower Fraser River, its estuary, and selected locations in Georgia Strait, British Columbia — 1972–73. Pestic. Monit. J. 9: 134–140.

ALLEN, R.L. 1977. Status of the upper Columbia River salmon and steelhead runs, p. 23–30. *In* E. Schwiebert [ed.] Columbia River salmon and steelhead. Am. Fish. Soc. Spec. Publ. 10. Wash., D.C.

ANDERSON, A.D., AND T.D. BEACHAM. 1983. The migration and exploitation of chum salmon stocks of the Johnstone Strait–Fraser River Study Area, 1962–1970. Can. Tech. Rep. Fish. Aquat. Sci. 1166: 125 p.

ANDREW, F.J., AND G.H. GEEN. 1960. Sockeye and pink salmon production in relation to proposed dams on the Fraser River system. *In* Pac. Salmon Fish. Comm. Bull. 11: 259 p.

ANDRIYASHEV, A. P. 1954. Fishes of the northern seas of the U.S.S.R. Zool. Inst., U.S.S.R. Acad. Sci., Keys to the fauna of the U.S.S.R. No. 53. (Transl. from Russian by Israel Prog. Sci. Transl., Jerusalem 1964), 617 p.

ANONYMOUS. 1963. Final report of the Fraser River Board on flood control and hydroelectric power in the Fraser River basin, Victoria, British Columbia. 106 p.

1973. The Mackenzie basin. Can. Inland Waters Directorate, Ottawa, Ont. 131 p.

1973–1982. Statistical Yearbook. Int. North Pac. Fish. Comm.

1974. Water quality data. British Columbia 1961–71. Environ. Can., Inland Waters Directorate, Ottawa, Ont.

1978. Fraser River Estuary Study Summary. Proposals for the development of an estuary management plan: summary report of the steering committee. Government of Canada, Province of British Columbia. Victoria, B.C. 145 p.

1979. Historical catch statistics for salmon of the North Pacific Ocean. Int. North Pac. Fish. Comm. Bull. 39: 166 p.

1980a. Pond fish culture in China. Pearl River Fisheries Research Institute, China National Bureau of Aquatic Products, Guanghzou, China, 136 p.

1980b. Freshwater aquaculture development in China. United Nations, FAO Fish. Tech. Pap. 215: 124 p.

1981. Mackenzie River basin study report. Mackenzie River Basin Committee, Federal-Provincial Study Agreement. 231 p.

1985. B. C. Debris Control Board Annual Report for the period April 1, 1984 to March 31, 1985. 11 p.

ARAI, H. P., AND D. R. MUDRY. 1983. Protozoan and metazoan parasites of fishes from the headwaters of the Parsnip and McGregor rivers, British Columbia: a study of possible parasite transfaunation. Can. J. Fish. Aquat. Sci. 40: 1676–1684.

ARMSTRONG, J. E., 1981. Post-Vashon Wisconsin glaciation, Fraser Lowland, British Columbia. Bull. Geol. Surv. Can. 322: 1–34.

ARO, K. V., AND M. P. SHEPARD. 1967. Salmon of the North Pacific Ocean. Part IV. Spawning populations of North Pacific Salmon. 5. Pacific Salmon in Canada. Int. North Pac. Fish. Comm. Bull. 23: 225–327.

ARRIGNON, J. 1972. Zonation piscicole de quelques cours d'eau normands (France). Verh. Int. Verein. Limnol. 18: 1135–1146.

BALON, E. K., S. S. CRAWFORD, AND A. LELEK. 1986. Fish communities of the upper Danube River (Germany, Austria) prior to the new Rhein-Main-Donau connection. Environ. Biol. Fishes 15: 243–271.

BAKKALA, R. G. 1970. Synopsis of biological data on the chum salmon, *Oncorhynchus keta* (Walbaum) 1792. U.S. Dept. Int., U.S. Fish & Wildlife Serv., Bur. Comm. Fish. Circ. 315, FAO Fisheries Synopsis 41: 89 p.

BAWDEN, C. A., W. A. HEATH, AND A. B. NORTON. 1973. A preliminary baseline study of Roberts and Sturgeon Banks. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 1: 54 p.

BEACHAM, T. D. 1984a. Catch, escapement, and exploitation of chum salmon in British Columbia, 1951–1981. Can. Tech. Rep. Fish. Aquat. Sci. 1270: 201 p.

1984b. Catch, escapement and exploitation of pink salmon in British Columbia. 1951–1981. Can. Tech. Rep. Fish. Aquat. Sci. 1276: 215 p.

BEACHAM, T. D., AND P. STARR. 1982. Population biology of chum salmon, *Oncorhynchus keta*, from the Fraser River, British Columbia. Fish. Bull. 80: 813–825.

BEACHAM, T.D., AND C. B. MURRAY. 1985. Variation in length and body depth of pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) in southern British Columbia. Can. J. Fish. Aquat. Sci. 42: 312–319.

1986. Comparative developmental biology of chum salmon (*Oncorhynchus keta*) from the Fraser River, British Columbia. Can. J. Fish. Aquat. Sci. 43: 252–262.

BEAMISH, R. J. AND J. R. SCARSBROOK. 1979. The distribution and feeding habits of lampreys in the surface waters of the Gulf Islands and in the vicinity of the Fraser River, British Columbia. Fish. Mar. Serv. MS Rep. 1512: 353 p.

BELL, C. R., AND L. J. ALBRIGHT. 1981. Attached and free-floating bacteria in the Fraser River estuary, British Columbia, Canada. Mar. Ecol. Prog. Ser. 6: 317–327.

BENEDICT, A. H., K. J. HALL, AND F. A. KOCH. 1973. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 2: 50 p.

BERG, L. S. 1948. Freshwater fishes of the U.S.S.R. and adjacent countries, Vol. 1. Fourth edition, Acad. Sci. U.S.S.R. Zool. Inst., Guide to the fauna of the U.S.S.R. No. 27, (Transl. from Russian by Israel Prog. Sci. Transl., Jerusalem). 504 p.

1949. Freshwater fishes of the U.S.S.R. and adjacent countries. Vol. III. Fourth edition, Acad. Sci. U.S.S.R. Zool. Inst. (Transl. from Russian by Israel Prog. Sci. Transl., Jerusalem. 1965). 510 p.

BILLINGS, S. J. 1982. Steelhead harvest analysis 1981–82. B. C. Min. Environ. Fish. Tech. Circ. 56: 26 p.

1983. Steelhead harvest analysis 1982–83. B. C. Min. Environ. Fish. Tech. Circ. 59: 23 p.

1984. Steelhead harvest analysis 1983–84. B. C. Min. Environ. Fish. Tech. Circ. 64: 21 p.

1986. Steelhead harvest analysis 1984–85. B. C. Min. Environ. Fish. Tech. Circ. 71: 99 p.

BIRTWELL, I. K., C. D. LEVINGS, J. S. MACDONALD, J. H. MUNDIE, AND I. H. ROGERS. 1986. A review of fish habitat issues in the Fraser River system. Unpublished manuscript, Canada Dep. Fish. Oceans, West Vancouver Laboratory, B. C.

BLUM, J. L. 1956. The ecology of river algae. Bot. Rev. 22: 291–341.

BORDEN, C. E. 1968. Prehistory of the Lower Mainland, p. 9–26. *In* A.H. Siemens [ed.] Lower Fraser Valley: evolution of a cultural landscape. B. C. Geograph. Ser. 9.

BRANNON, E. L. 1972. Mechanisms controlling migration of sockeye salmon fry. Int. Pac. Salmon Fish. Comm. Bull. 21: 6 p.

BRENNER, T. 1984. The introduction of Arctic charr (*Salvelinus alpinus salvelinus*) in Nordrhein Westfalen (Federal Republic of Germany), p. 293–301. *In* L. Johnson and B. Burns [ed.] Biology of the Arctic charr: Proc. Int. Symp. on Arctic charr. Univ. Manitoba Press, Winnipeg. Man.

Buklis, L. S. 1981. Yukon and Tanana River fall chum salmon tagging study, 1976–1980. Alaska Dep. Fish & Game Inform. Leaf. 194: 40 p.

Buklis, L. S., and L. H. Barton. 1984. Yukon River fall chum salmon biology and stock status. Alaska Dep. Fish & Game Inform. Leaf. 239: 67 p.

Burr, B.M., and L. M. Page. 1986. Zoogeography of fishes of the lower Ohio-Upper Mississippi basin, p. 287–324. *In* C. H. Hocutt and E. O. Wiley [ed.] The zoogeography of North American freshwater fishes. John Wiley & Sons, New York, NY.

Busnita, T. 1967. Die ichthyofauna des Donauflusses, p. 198–224. *In* R. Liepolt [ed.] Limnologie der Donau. Leifg. 3, E. Schweizerbart'sche Verlagsbuchandlung, Stuttgard.

Cavender, T. M. 1978. Taxonomy and distribution of the bull trout, *Salvelinus confluentus* (Suckley), from the American northwest. Calif. Fish & Game 64: 139–174.

Chapman, P. M., L. M. Churchland, P. A. Thompson, and E. Michnowsky. 1980. Heavy metal studies with oligochaetes, p. 477-502. *In* R. O. Brinkhurst and D. G. Cook [ed.] Aquatic oligochaete biology. Plenum Publ. Co.

Chapman, P. M., and R.O. Brinkhurst. 1981. Seasonal changes in interstitial salinities and seasonal movements of subtidal benthic invertebrates in the Fraser River estuary, B. C. Estuarine, Coastal and Shelf Sci. 12: 49–66.

Christie, W. J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board. Can. 31: 827–854.

Churchland, L. M., and G. Kan. 1982. Variation in fecal pollution indicators through tidal cycles in the Fraser River estuary. Can. J. Microbiol. 28: 239–247.

Clague, J. J., J. E. Armstrong, and W. H. Mathews. 1980. Advance of the Late Wisconsin Cordilleran ice sheet in southern British Columbia since 22,000 B. P. Quart. Res. 13: 322–326.

Clark, M. J. R., T. O. Morrison, A. Nugent, G. R. Gough, D. W. Holmes, and D. H. G. Ableson. 1981. A preliminary study of water quality in the Fraser River and its tributaries. British Columbia Min. Environ., Waste Manage. Branch Rep. 80-12: 301 p.

Cooper, A. C. 1977. Evaluation of the production of sockeye and pink salmon at spawning and incubation channels in the Fraser River system. Int. Pac. Salmon Fish. Comm. Prog. Rep. 36: 80 p.

Cross, F. B., R. L. Mayden, and J. D. Stewart. 1986. Fishes in the western Mississippi basin (Missouri, Arkansas, and Red Rivers), p. 363–412. *In* C. H. Hocutt and E. O. Wiley [ed.] The zoogeography of North American freshwater fishes. John Wiley & Sons, New York, NY.

Crossman, J. E., and D. E. McAllister. 1986. Zoogeography of freshwater fishes of the Hudson Bay drainage, Ungava Bay and the Arctic archipelago, p. 53–104. *In* C. H. Hocutt and E. O. Wiley [ed.] The zoogeography of North American freshwater fishes. John Wiley & Sons, New York, NY.

Cushing, C. E., and L. A. Rancitelli. 1972. Trace element analysis of Columbia River water and phytoplankton. Northwest Sci. 46: 115–121.

Delaney, P. W., A. L. Kahl, W. R. Olmsted, and P. C. Pearce. 1982. Studies of chinook salmon (*Oncorhynchus tshawytscha*) in the Chilcotin River watershed 1975–1980. Can. MS Rep. Fish. Aquat. Sci. 1674: 51 p.

Derksen, G. 1981. Environmental review of the Northwood, Intercontinental and Prince George pulpmills at Prince George, B. C. Can. Environ. Protection Branch, Pac. Reg., Reg. Prog. Rep. 82-4: 77 p.

Dixon, B. M. 1986. Age, growth and migration of white sturgeon in the Nechako and Upper Fraser rivers of British Columbia. B. C. Min. Environ. Fish. Tech. Circ. 70: 27 p.

Dorcey, A. H. J. [ed.]. 1976. The uncertain future of the Lower Fraser. Vancouver, Westwater Research Centre, The University of British Columbia. 202 p.

1986. C. E. A., and Management in the Fraser Estuary, p. 65 A1–A38. *In* N. C. Sonntag, R. R. Everitt, L. P. Rattie, D. L. Colnett, C. P. Wolf, J. Truett, A. H. J. Dorcey, C. S. Holling [ed.] Cumulative effects assessment; a context for further research and development. A report to Canadian Environmental Assessment Research Council, Ottawa, 99 p.

Drent, R., R. Gibbon, and J. Ward. 1971. Progress report. Gull and dunlin study in Vancouver Region. *In* Minutes of 5th meeting, Exec. Comm., Assoc. Comm. on Bird Hazards to Aircraft, June, 1972 (cited by Taylor 1974).

Dussart, B. H., K. F. Lagler, P. A. Larkin, T. Scudder, K. Szesztay, and G. F. White. 1972. Man-made lakes as modified ecosystems. Int. Council Sci. Unions. SCOPE Rep. 2: 76 p.

Dwernychuk, L.W. 1984. Water quality and benthic invertebrate studies in the Fraser River near Prince George 1963–1981; IEC Beak Consultants Ltd., Richmond, British Columbia. Vol. 1: 103 p. & tables, figures; Vol. 2, appendices.

Emery, L. 1981. Range extension of pink salmon (*Oncorhynchus gorbuscha*) into the lower Great Lakes. Fisheries 6(2): 7–10.

Ertl, M., S. Juris, and J. Tomajka. 1972. Vorlaufige angaben iche jahrezeit liche veranderungen und die vertikale verteilung des periphytons in mittelerren abshnitt der Donau. Arch. Hydrobiol. (Suppl. 44): 34–48.

Fairbairn, B., and K. Peterson. 1975. Controlling sawlog debris in the lower Fraser River. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 5: 35 p.

Farley, A. L. 1979. Atlas of British Columbia. Univ. British Columbia Press, Vancouver, B. C. 136 p.

Foerster, R. E. 1925. Studies in the ecology of the sockeye salmon (*Oncorhynchus nerka*). Contrib. Can. Biol. 2: 335–422.

Foerster, R. E. 1938. An investigation of the relative efficiencies of natural and artificial propagation of sockeye salmon (*Oncorhynchus nerka*) at Cultus Lake, British Columbia. J. Fish. Res. Board Can. 4: 151-161.

1968. The sockeye salmon, *Oncorhynchus nerka*. Bull. Fish. Res. Board Can. 162: 422 p.

Ford, B. S. 1982. Steelhead harvest analysis 1980–81. B. C. Min. Environ. Fish. Tech. Circ. 52: 87 p.

Fraser, F. J., P. J. Starr, and A. Y. Fedorenko, 1982. A review of the chinook and coho salmon of the Fraser River. Can. Tech. Rep. Fish. Aquat. Sci. 1126: 130 p.

Fry, D. H.. 1973. Anadromous fishes of California. Calif. Fish and Game, 111 p.

1977. Information on California salmon fisheries and stocks. Int. North Pac. Fish. Comm. Bull. 36: 15–23.

Fulton, L. A. 1970. Spawning areas and abundance of steelhead trout and coho, sockeye, and chum salmon in the Columbia River — past and present. U.S. Dep. Comm., Nat. Oceanic and Atmosp. Admin., Spec. Sci. Rep., Fish. 618: 37 p.

Fulton, R. J. 1969. Glacial lake history, southern interior plateau, British Columbia. Geol. Surv. Can. Pap. 69–37: 14 p.

Gaboury, M. N., and G. K. Spence. 1981. A report on the 1980 survey of brook trout (*Salvelinus fontinalis*) populations in remote lower Nelson River tributaries. Can. Dep. Nat. Resources, Fish. Branch, MS Rep. Dep. Nat. Resources (Manitoba) 81-16: 41 p.

Garrett, C. L. 1980. Fraser River estuary study. Water quality. Toxic organic contaminants. Government of Canada and Province of British Columbia, Vancouver, B. C. 125 p.

Geen, G. H. 1975. Ecological consequences of the proposed Moran Dam on the Fraser River. J. Fish. Res. Board Can. 32: 126–135.

Geen, G. H., and F. J. Andrew. 1961. Limnological changes in Seton Lake resulting from hydroelectric diversions. Int.

Pac. Salmon Fish Comm. Prog. Rep. 8: 76 p.

Geesey, G. G., L. Borstard, and P. M. Chapman. 1984. Influence of flow-related events on concentration and phase distribution of metals in the lower Fraser River and a small tributary stream in British Columbia, Canada. Water Res. 18: 233–238.

Gilhousen, P. 1980. Energy sources and expenditures in Fraser River sockeye salmon during their spawning migration. Int. Pac. Salmon Fish. Comm. Bull. 22: 51 p.

Golterman, H. L. 1975. Chemistry, p. 39–80. *In* B. A. Whitton [ed.] River Ecology. Univ. Calif. Press, Berkeley.

Goodlad, J. C., T. W. Gjernes, and E. L. Brannon. 1974. Factors affecting sockeye salmon (*Oncorhynchus nerka*) growth in four lakes of the Fraser River system. J. Fish. Res. Board Can. 31: 871–892.

Gordon, D. K., and C. D. Levings. 1984. Seasonal changes of inshore fish populations on Sturgeon and Roberts Bank, Fraser River estuary, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1240: 81 p.

Grieve, D. A., and W. K. Fletcher. 1976. Heavy metals in deltaic sediment of the Fraser River, British Columbia. Can. J. Earth Sci. 13: 1683–1693.

Gunsolus, R. T. 1977. Status of the salmon and steelhead runs entering the Columbia River, p. 21–22. *In* E. Schwiebert [ed.] Columbia River salmon and steelhead. Am. Fish. Soc. Spec. Publ. 10, Wash., D. C.

Haig-Brown, R. 1972. The Fraser watershed and the Moran proposal. Nature Can. 1: 2–10.

Hall, K. J. 1986. A review of toxic substances in the Fraser River estuary, p. 1–47. *In* F. Mah and M. McPhee [Compilers] Toxic chemical research needs in the Lower Fraser River, Workshop Proceedings, Univ. British Columbia, 19 June 1985, Environment Canada.

Hall, K. J., F. A. Koch, and I. Yesaki. 1974. Further investigations into water quality conditions in the Lower Fraser River system. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 4: 104 p.

Hall, K. J., I. Yesaki, and J. Chan. 1976. Trace metals and chlorinated hydro-carbons in the sediments of a metropolitan watershed. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 10: 74 p.

Halladay, D. R., and R. D. Harris. 1972. A commitment to the future — a proposal for the protection and management of the Fraser weltlands. British Columbia Fish & Wildlife and Canadian Wildlife Service. 17 p.

Hallock, R. J., and D. H. Fry. 1967. Five species of salmon, *Oncorhynchus*, in the Sacramento River, California. Calif. Fish & Game 53: 5–22.

Hallock, R. J., W. F. Van Woert, and L. Shapovalov. 1961. An evaluation of stocking hatchery-reared steelhead rainbow trout (*Salmo gairdneri*) in the Sacramento River system. Calif. Dep. Fish & Game, Fish. Bull. 114: 74 p.

Healey, M. C. 1982. Catch, escapement and stock recruitment for British Columbia chinook salmon since 1951. Can. Tech. Rep. Fish. Aquat. Sci. 1107: 77 p.

MS, The life-history of chinook salmon. *In* C. Groot and L. Margolis [ed.] Life history of Pacific salmon. Can. Bull. Fish. Aquat. Sci. (In preparation)

Hensel, K. 1980. The occurrence of brook trout — *Salvelinus fontinalis* in the main stream of the Danube River. Vestn. Cesk. Spol. Zool. 44: 39 p.

Holčík, J., I. Bastl, M. Ertl, and M. Vranovsky. 1981. Hydrobiology and ichthyology of the Czechoslovak Danube in relation to predicted changes after the construction of the Gabcikovo-Nagymaros River barrage system. Pr. Lab. Rybarstva Hydrobiol. 3: 19–158.

Hutchinson, B. 1950. The Fraser. Rinehart and Co. Inc., U.S.A. 368 p.

Illies, J. [ed.] 1978. Limnofauna europaea. 2. Auflage. Gustav Fischer Verlag, Stuttgart. 532 p.

Jackson, K. [ed.] 1984. Toward a fish habitat decision on the Kemano completion project: a discussion paper. Can. Fish. Oceans. Habitat Manage. Division. Vancouver, B. C. 77 p.

Johnston, N. T., L. J. Albright, T. G. Northcote, P. C. Oloffs, and K. Tsumura. 1975. Chlorinated hydrocarbon residues in fishes from the lower Fraser River. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 9: 31 p.

Joy, C. S. 1975. Water quality models of the Lower Fraser River. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 6: 52 p.

Jungwirth, M. 1978. Some notes to the farming and conservation of the Danube salmon (*Hucho hucho*). Environ. Biol. Fish. 3: 231–234.

Kasahara, H. 1961. Fisheries resources of the North Pacific Ocean. H. R. MacMillan Lectures in Fisheries, Inst. Fisheries, Univ. British Columbia, Vancouver, B. C. 135 p.

Kistritz, R. U. 1978. An ecological evaluation of Fraser estuary tidal marshes: the role of detritus and the cycling of elements. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 15: 59 p.

Kolder, W. 1966. Der Fischbestand der oberen Wisla und seine Veranderungen nach der Erbauung des Staubeckens Gaczalkowice. Verh. Int. Verein. Limnol. 16: 1228–1236.

Korn, L. 1977. Information on Columbia River salmon runs and fisheries. Int. North Pac. Fish. Comm. Bull. 36: 1–14.

Kwain, W. 1982. Spawning behavior and early life history of pink salmon (*Oncorhynchus gorbuscha*) in the Great Lakes. Can. J. Fish. Aquat. Sci. 39: 1353–1360.

Kwain, W., and A. H. Lawrie. 1981. Pink salmon in the Great Lakes. Fisheries 6: 2–6.

Ladiges, W., and D. Vogt. 1979. Die susswasserfische europas. Paul Parey, Hamburg. 299 p.

Lack, T. J. 1971. Quantitative studies on the phytoplankton of the rivers Thames and Kennet at Reading. Freshwater Biol. 1: 213–224.

Lake, J. S. 1967. Principal fishes of the Murray-Darling River system, p. 192-213. *In* A. H. Weatherley [ed.] Australian inland waters and their fauna. Australian Nat. Univ. Press. Canberra.

1971. Freshwater Fishes and Rivers of Australia. Thomas Nelson (Australia) Ltd., Sydney. 61 p.

Larkin, P. A. 1970. Management of Pacific Salmon in North America, p. 223–236. *In* N. G. Benson [ed.] A century of fisheries in North America. Am. Fish. Soc. Spec. Publ. 7. Washington, D. C.

Larkin, P. A., and W. E. Ricker. 1964. Canada's Pacific marine fisheries; past performance and future prospects, p. 194–268. *In* Inventory of the Natural Resources of British Columbia. 15th British Columbia Nat. Res. Conf.

Larkin, P. A., and J. G. McDonald. 1968. Factors in the population biology of the sockeye salmon of the Skeena River. J. Anim. Ecol. 37: 229–258.

Lawrie, A. H., and J. F. Rahrer. 1972. Lake Superior: effects of exploitation and introductions on the salmonid community. J. Fish. Res. Board Can. 29: 765–776.

Levings, C. D. 1982. Short term use of a low tide refuge in a sandflat by juvenile chinook, (*Oncorhynchus tshawytscha*), Fraser River estuary. Can. Tech. Rep. Fish. Aquat. Sci. 1111: 33 p.

Levings, C. D., and J. B. Coustalin. 1975. Zonation of intertidal biomass and related benthic data from Sturgeon and Roberts Banks, Fraser River estuary, British Columbia. Can. Fish. Mar. Serv. Tech. Rep. 468: 138 p.

Levy, D. A., T. G. Northcote, and G. J. Birch. 1979. Juvenile salmon utilization of tidal channels in the Fraser River estuary, British Columbia. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 23: 70 p.

Levy, D. A., and T. G. Northcote. 1981. The distribution and abundance of juvenile salmon in marsh habitats of the Fraser River estuary. Univ. British Columbia, Westwater, Res. Centre Tech. Rep. 25: 117 p.

1982. Juvenile salmon residency in a marsh area of the Fraser River estuary. Can. J. Fish. Aquat. Sci. 39: 270–276.

Levy, D. A., T. G. Northcote, and R. M. Barr. 1982. Effects of estuarine log storage on juvenile salmon. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 26: 101 p.

Li, Sizhong. 1984. Discussion on the geographical distribution of salmonid fishes in China. Chinese J. Zool. 1984 (1): 34–37.

Lindsey, C. C. 1957. Possible effects of water diversions of fish distribution in British Columbia. J. Fish. Res. Board. Can. 14: 651–668.

Lindsey, C. C., and J. D. McPhail. 1986. Zoogeography of fishes of the Yukon and Mackenzie basins, p. 639–674. *In* C. H. Hocutt and E. O. Wiley [ed.] The zoogeography of North American freswhater fishes. John Wiley & Sons, New York, NY.

Lyons, C. 1969. Salmon: our heritage. Mitchell Press, Vancouver, B. C. 768 p.

MacCrimmon, H. R. 1971. World distribution of rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 28: 663–704.

MacCrimmon, H. R., and T. L. Marshall. 1968. World distribution of brown trout, *Salmo trutta*. J. Fish. Res. Board Can. 25: 2527–2548.

MacCrimmon, H. R., and J. S. Campbell. 1969. World distribution of brook trout, *Salvelinus fontinalis*. J. Fish. Res. Board Can. 26: 1699–1725.

Machidori, S., and F. Kato. 1984. Spawning populations and marine life of masu salmon (*Oncorhynchus masou*). Int. North Pac. Fish. Comm. Bull. 43: 138 p.

MacLennan, H. 1974. Rivers of Canada. MacMillan Co. of Canada Ltd., Toronto, Ont. 270 p.

Martell, A. M., D. M. Dickinson, and L. M. Casselman. 1984. Wildlife of the Mackenzie delta region. Boreal Inst. Nor. Studies, University of Alberta, Edmonton, Occas. Publ. 15: 214 p.

Mathews, W. H., and F. P. Shepard. 1962. Sedimentation of the Fraser River delta, British Columbia. Bull. Am. Assoc. Petrol. Geol. 46: 1416–1443.

Mathews, W. H., J. G. Fyles, and H. W. Nasmith. 1970. Postglacial crustal movements in southwestern British Columbia and adjacent Washington State. Can. J. Earth Sci. 7: 690–702.

Mauney, J. L., and M. Geiger. 1977. Yukon River anadromous fish investigations: Yukon River king and chum salmon escapements studies. Alaska Dept. Fish & Game, Juneau, Alaska for Nat'l. Marine Fish. Serv., Wash., D. C. NOAA-78042701.

McCart, P. J., and J. D. Beste. 1979. Aquatic resources of the Northwest Territories. Sci. Advisory Bd. N.W.T., Yellowknife. 55 p.

McLeod, C. L., and J. P. O'Neil. 1983. Major range extensions of anadromous salmonids and first record of chinook salmon in the Mackenzie River drainage. Can. J. Zool. 61: 2183–2184.

McLeod, G. D. 1979. McGregor River diversion Fraser River temperature study. Can. Soc. Civil Eng. 4th Nat. Hydrotech. Conf. River Basin Manage., p. 180–195.

McPhail, J. D., and C. C. Lindsey. 1986. Zoogeography of the freshwater fishes of cascadia (the Columbia system and rivers north to the Stikine), p. 615–637. *In* C. H. Hocutt and E. O. Wiley [ed.] The zoogeography of North American freshwater fishes. John Wiley & Sons, New York, N. Y.

Meyer, P. A. 1978. Updated estimates for recreation and preservation values associated with the salmon and steelhead of the Fraser River. Fish. Environ. Can., Habitat Protection Directorate, Pac. Reg. 36 p.

Milligan, P. A., W. O. Rublee, D. D. Cornett, and R. A. C. Johnstone. 1984. The distribution and abundance of chinook salmon (*Oncorhynchus tshawytscha*) in the upper Yukon River basin as determined by a radio-tagging and spaghetti tagging program: 1982–1983. Can. Tech. Rep. Fish. Aquat. Sci. 1352: 161 p.

1986. The distribution and abundance of chum salmon (*Oncorhynchus keta*) in the upper Yukon River basin as determined by a radio-tagging and spaghetti tagging program: 1982–1983. Can. Tech. Rep. Fish. Aquat. Sci. 1351: 141 p.

Minckley, W. L., D. A. Hendrickson, and C. E. Bond. 1986. Geography of western North American freshwater fishes: description and relationships to intracontinental tectonism, p. 519–613. *In* C. H. Hocutt and E. O. Wiley [ed.] The zoogeography of North American freshwater fishes. John Wiley & Sons, New York, NY.

Moore, D. C., and W. R. Olmsted. 1985. Thompson River steelhead angler survey — 1984. Howard Paish and Assoc. Ltd. 39 p. + appendices.

Narver, D. W. 1977. Benefits and future of wild steelhead — the British Columbia scene, p. 51-58. *In* E. Schwiebert [ed.] Columbia River salmon and steelhead. Am. Fish. Soc. Spec. Publ. 10. Wash., D. C.

Nelson, J. S. 1984. Fishes of the World. 2nd ed. John Wiley & Sons, Ltd., New York, NY, 523 p.

Nelva, A., E. Pattee, J. F. Perrin, H. Persat, et A.L. Roux. 1981. Structure et fonctionnement des écosystèmes du Haut-Rhone français. 25. Premières observations sur les populations piscicoles dans le secteur de Bregnier-Cordon. Verh. Int. Verein. Limnol. 21: 1276–1282.

Netboy, A. 1973. The Salmon — their fight for survival. Houghton Mifflin Co., Boston, MA. 613 p.

1980. The Columbia River Salmon and Steelhead Trout — their fight for survival. Univ. Washington Press, Seattle, WA. 180 p.

Nichols, J. T. 1943. The fresh-water fishes of China. Natural history of Central Asia. Vol. IX. Am. Mus. Nat. History, New York, NY, 322 p.

Northcote, T. G. 1974. Biology of the lower Fraser River: a review. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 3: 94 p.

1976. Biology of the lower Fraser and ecological effects of pollution, p. 85–119. *In* A.H.J. Dorcey [ed.] The uncertain future of the Lower Fraser. Univ. British Columbia, Westwater Res. Centre.

Northcote, T. G., and P. A. Larkin. 1956. Indices of productivity in British Columbia lakes. J. Fish. Res. Board Can. 13: 515–540.

1963. Western Canada, p. 451–485. *In* D. G. Frey [ed.] Limnology in North America. Univ. Wisconsin Press, Madison, WI., USA.

Northcote, T. G., G. L. Ennis, and M. H. Anderson. 1975a. Periphytic and planktonic algae of the lower Fraser River in relation to water quality conditions. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 8: 61 p.

Northcote, T. G., N. T. Johnston, and K. Tsumura. 1975b. Trace metal concentrations in lower Fraser River fishes. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 7: 41 p.

1976. Benthic, epibenthic and drift fauna of the lower Fraser River. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 11: 227 p.

1978. A regional comparison of species distribution, abundance, size and other characteristics of lower Fraser River fishes. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 14: 38 p.

1979. Feeding relationships and food web structure of lower Fraser River fishes. Univ. British Columbia. Westwater Res. Centre Tech. Rep. 16: 73 p.

OLOFFS, P. C., L. J. ALBRIGHT, AND S. Y. SZETO. 1972. Fate and behaviour of five chlorinated hydrocarbons in three natural waters. Can. J. Microbiol. 18: 1393–1398.

O'NEILL, M., AND V. LEWYNSKY. 1985. Lower Skeena creel survey 1984. Howard Paish and Assoc. Ltd. 16 p.

ORMSBY, M. A. 1958. British Columbia: a history. MacMillan Canada, Evergreen Press, Vancouver, B.C. 558 p.

PALMER, R. N. 1972. Fraser River chum salmon. Can. Dep. Environ. Fish. Serv. Tech. Rep. 1972–1: 248 p.

PARSONS, T. R., R. J. LEBRASSEUR, AND W. E. BARRACLOUGH. 1970. Levels of production in the pelagic environment of the Strait of Georgia, British Columbia: a review. J. Fish. Res. Board Can. 27: 1251–1264.

PAUTZKE, C. F., AND R. C. MEIGS. 1940. Studies on the life history of the Puget Sound steelhead trout (*Salmo gairdneri*). Trans. Am. Fish. Soc. 70: 209–220.

PEARSE, P. H. 1982. Turning the tide. A new policy for Canada's Pacific fisheries. Final Rep., Comm. Pac. Fish. Policy. 292 p.

PENAZ, M. 1966. Einfluss der Talsperren auf die Ichthyofauna der unterhalb und oberhalb des Sausees liegenden Flussabschnitte. Verh. Int. Verein. Limnol. 16: 1223–1227.

PERCY, R. 1975. Fishes of the outer Mackenzie delta. British Columbia Dept. Environ., Beaufort Sea Tech. Rep. 8: 114 p.

PETERSON, G. R., AND J. C. LYONS. 1968. A preliminary study of steelhead in the Big Qualicum River. B.C. Fish & Wildl. Br. Manage. Rep. 56: 46 p.

POMEROY, W. M., AND C. D. LEVINGS. 1980. Association and feeding relationships between *Eogammarus confervicolus* (Amphipoda, Gammaridae) and benthic algae on Sturgeon and Roberts Banks, Fraser River estuary. Can. J. Fish. Aquat. Sci. 37: 1–10.

PODDUBNYI, A. G. 1979. The ichthyofauna of the Volga, p. 304–339. *In* P. D. Mordukhai-Boltovoskoi [ed.] The River Volga and its life. Dr. W. Junk bv Publishers, The Hague.

PRAWOCHENSKSY, R., AND W. KOLDER. 1968. Synopsis of biological data on *Hucho hucho* (Linnaeus, 1758). United Nations, FAO Fisheries Synopsis 22 (Suppl. 1): 27 p.

RICKER, W. E. 1937a. Physical and chemical characteristics of Cultus Lake, British Columbia. J. Biol. Board Can. 3: 363–402.

1937b. The food and food supply of sockeye salmon (*Oncorhynchus nerka*, Walbaum) in Cultus Lake, British Columbia. J. Biol. Board Can. 3: 450–468.

1950. Cyclic dominance among the Fraser River sockeye. Ecology 31: 6–26.

RICKER, W. E., AND J. I. MANZER. 1974. Recent information on salmon stocks in British Columbia. Int. North Pac. Fish. Comm. Bull. 29: 1–24.

ROBINSON, J. L. 1985. Fraser River, p. 692. *In* The Canadian Encyclopedia. Vol. 2, Hurtig Publishers, Edmonton.

ROCCHINI, R. J., R. W. DRINNAN, D. E. STANCIL, L. G. SWAIN, M.J.R. CLARK, L. M. CHURCHLAND, W. E. ERLEBACH, O. E. LANGER, D. G. DELVIN, AND S. A. VERNON. 1979. Fraser River estuary study, Water quality; Summary Report of the Water Quality Working Group. Government of Canada and Province of British Columbia, Victoria, B. C. 176 p.

ROGERS, I. H., AND H. W. MAHOOD. 1982. Environmental monitoring of the Fraser River at Prince George. Chemical analysis of fish, sediment, municipal sewage and bleached Kraft wastewater samples. Can. Tech. Rep. Fish. Aquat. Sci. 1135: 15 p.

SANO, S. 1967. Salmon of the North Pacific Ocean. Part IV. Spawning populations of North Pacific salmon. 3. Chum salmon in the Far East. Int. North Pac. Fish. Comm. Bull. 23: 23–41.

SAVVAITOVA, K. A., AND V. A. MAKSIMOV. 1980. Forms' origination in chars of the genus *Salvelinus* (Salmoniformes, Salmonidae) from the Lena delta lakes. Zool. Zh. 59: 1820–1830.

SCHULZ, N. 1985. Das wachstum des huchens (*Hucho hucho* L.) in der Drau in Kaernten. Oesterr. Fisch. 38: 133–142.

SCHULZ, N., AND G. PIERY. 1982. Zur fortpflanzung des Huchens (*Hucho hucho* L.) Untersuchung einer Laichgrabe. Oesterr. Fisch. 35: 241–249.

SCOTT, K. J. 1985. Angler use and catch survey of anadromous trout fisheries in the lower Fraser River, 1984/85. Howard Paish and Assoc. Ltd. 34 p. + appendices.

SCOTT, K. J., AND V. A. LEWYNSKY. 1985. Angler use and catch survey of the Chilliwack-Vedder River steelhead fishery, 1985. Howard Paish and Assoc. Ltd. 21 p. + appendices.

SEAGEL, G. C., AND M. F. PUGH. 1981. A perspective on water transfer: McGregor diversion project. Can. Water Resour. J-6: 76–88.

SEMAKULA, S. N., AND P. A. LARKIN. 1968. Age, growth, food and yield of the white sturgeon (*Acipenser transmontanus*) of the Fraser River, British Columbia. J. Fish. Res. Board. Can. 25: 2589–2602.

SERVIZI, J. A., R. W. GORDON, AND D. W. MARTENS. 1968. Toxicity of two chlorinated catechols, possible components of Kraft pulp mill bleach waste. Int. Pac. Salmon Fish. Comm. Prog. Rep. 17: 43 p.

SERVIZI, J. A., AND R. A. BURKHLATER. 1970. Selected measurements of water quality and bottom-dwelling organisms of the Fraser River system 1963 to 1968. Int. Pac. Salmon Fish. Comm. MS Rep. 70 p.

SHEPARD, M. P., C. D. SHEPARD, AND A. W. ARGUE. 1985. Historic statistics of salmon production around the Pacific rim. Can. MS Rep. Fish. Aquat. Sci. 1819: 297 p.

SMITH, S. H. 1972. Factors of ecological succession in oligotrophic fish communities of the Laurentian Great Lakes. J. Fish. Res. Board Can. 29: 717–730.

SPILLMAN, C. J. 1961. Faune de France. 65. Poissons d'eau douce. Librairie Fac. Sci., Paris. 303 p.

STARR, P. J., A. T. CHARLES, AND M. A. HENDERSON. 1984. Reconstruction of British Columbia sockeye salmon (*Oncorhynchus nerka*) stocks: 1970–1982. Can. MS Rep. Fish. Aquat. Sci. 1780: 123 p.

STEIN, J. N., C. S. JESSOP, T. R. PORTER, AND K. T. J. CHANG-KUE. 1973. An evaluation of the fish resources of the Mackenzie River valley as related to pipeline development. Vol. 1. Can. Dep. Environ., Fish. Serv. 121 p.

STEWART, D. J., J. F. KITCHELL, AND L. B. CROWDER. 1981. Forage fishes and their salmonid predators in Lake Michigan. Trans. Am. Fish. Soc. 110: 751–763.

ST. JOHN, B. E., E. C. CARMACK, R. J. DALEY, C. B. J. GRAY, AND C. H. PHARO. 1976. The limnology of Kamloops Lake. Can. Inland Waters Directorate, Vancouver, B. C. 167 p.

STOCKNER, J. G., AND K. S. SHORTREED. 1983. A comparative limnological survey of 19 sockeye salmon (*Oncorhynchus nerka*) nursery lakes in the Fraser River system, British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 1190: 63 p.

STONE, D., T. C. GRIFFING, AND M. C. KNIGHT. 1974. Biological monitoring of the Fraser River near Prince George, B. C. Pulp Paper Mag. Can. 75(C): T110–T116.

STONE, M. 1982. Fresh water sport fishing in British Columbia: an overview of the 1980 national survey of sports fishing. British Columbia Min. Environ., Planning Branch, Victoria, B. C. 90 p.

TAYLOR, E. B., AND P. A. LARKIN. 1986. Current response and agonistic behavior in newly emerged fry of chinook salmon, *Oncorhynchus tshawytscha*, from ocean – and stream-type populations. Can. J. Fish. Aquat. Sci. 43: 565–573.

TAYLOR, E. B., AND J. D. MCPHAIL. 1985a. Variation in body morphology among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Can. J. Fish. Aquat. Sci. 42: 2020–2028.

1985b. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Can. J. Fish. Aquat. Sci. 42:

2029–2033.

TAYLOR, E. W. 1974. The Vancouver International airport expansion proposals and possible impact on wildlife of the Fraser River estuary. Can. Wildlife Serv., Delta, B.C. 54 p.

THOMPSON, ANDREW R. 1986. Planning for the Fraser–Thompson corridor — a clash of perspectives. Paper presented to annual meeting Canadian Inst. Planners. 16 p.

THORP, C. 1985. Detailed surface water quality data. British Columbia 1979–81. Can. Inland Waters Directorate, Vancouver, B. C. 58 p.

TIPPER, H. W. 1971. Glacial geomorphology and Pleistocene history of central British Columbia. Bull. Geol. Surv. Can. 196: 1–89.

TSUYUKI, H., AND S. N. WILLISCROFT. 1977. Swimming stamina differences between genotypically distinct forms of rainbow (*Salmo gairdneri*) and steelhead trout. J. Fish. Res. Board Can. 34: 996–1003.

UNDERHILL, J. C. 1986. The fish fauna of the Laurentian Great Lakes, the St. Lawrence lowlands, Newfoundland and Labrador, p. 105–136. *In* C. H. Hocutt and E. O. Wiley [ed.] The zoogeography of North American freshwater fishes. John Wiley & Sons, New York, NY.

VAN HYNING, J. M. 1973. Stock–recruitment relationships for Columbia River chinook salmon, p. 89–97. *In* B. B. Parrish [ed.] Fish stocks and recruitment. Cons. Int. l'Expl. Mer., Rapp. et Proc. des Réunions Vol. 164.

VINCENT, F. 1980. Columbia basin anadromous salmonid fisheries, p. 486–492. *In* J. H. Grover [ed.] Allocation of fishery resources. Proc. Tech. Consul. Alloc. Fish. Resources, United Nations FAO and Am. Fish. Soc.

VOLLENWEIDER, R. A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication. O.E.C.D., Paris. 193 p.

WAGNER, W. C., AND T. M. STAUFFER. 1982. Distribution and abundance of pink salmon in Michigan tributaries of the Great Lakes, 1967–1980. Trans. Am. Fish. Soc. 111: 523–526.

WARD, F. J. 1957. Seasonal and annual changes in availability of the adult crustacean plankters of Shuswap Lake. Int. Pac. Salmon Fish. Comm. Prog. Rep. 3: 56 p.

1966. Initiation of vernal heating in Kamloops Lake, B. C. Verh. Int. Verein. Limnol. 16: 111–117.

WARD, F. J., AND P. A. LARKIN. 1964. Cyclic dominance in Adams River sockeye salmon. Int. Pac. Salmon Fish. Comm. Prog. Rep. 11: 116 p.

WEATHERLEY, A. H., AND J. S. LAKE. 1967. Introduced fish species in Australian inland waters, p. 217–239. *In* A. H. Weatherley [*ed.*] Australian inland waters and their fauna. Australian Nat. Univ. Press, Canberra.

WEHRHAHN, C. F., AND R. POWELL. 1987. Electrophoretic variation, regional differences, and gene flow in the coho salmon (*Oncorhynchus kisutch*) of southern British Columbia. Can. J. Fish. Aquat. Sci. 44: 822–831.

WELCOMME, R. L. 1985. River fisheries. FAO, United Nations. Rome. Fish. Tech. Pap. 262: 330 p.

WHITFIELD, P. H. 1983. Regionalization of water quality in the upper Fraser River basin, British Columbia. Water Res. 17: 1053–1066.

WHITFIELD, P. H., AND H. SCHREIER. 1981. Hysteresis in relationships between discharge and water chemistry in the Fraser River basin, British Columbia. Limnol. Oceanogr. 26: 1179–1182.

WILLIAMS, I. 1976. Preliminary report on efforts to establish an even–year pink salmon run on the Fraser River, p. 127–128. *In* G. A. Gunstrom [ed.] Proceedings of the 1976 Northeast Pacific Pink and Chum Salmon Workshop, Juneau, Alaska.

WILLIAMS, L. G. 1964. Possible relationship between plankton–diatom species numbers and water–quality estimates. Ecology 45: 809–823.

1972. Plankton diatom species biomasses and the quality of American rivers and the Great Lakes. Ecology 53: 1038–1050.

WILLIAMS, L. G., AND C. SCOTT. 1962. Principal diatoms of major waterways of the United States. Limnol. Oceanogr. 7: 365–379.

WILSON, M. V. H. 1977a. Middle Eocene freshwater fishes from British Columbia. Royal Ontario Museum, Life Sciences Contributions 113: 61 p.

WILSON, M. V. H. 1977b. Paleoecology of Eocene lacustrine varves at Horsefly, British Columbia. Can. J. Earth Sci. 14: 953–962.

1980. Eocene lake environments: depth and distance–from–shore variation in fish, insect and plant assemblages. Paleogeogr., Palaeoclim., Paleoecol. 32: 21–44.

1984. Year classes and sexual dimorphism in the Eocene catostomid fish *Amyzon aggregatum*. J. Vert. Paleontology 3: 137–142.

YAMANAKA, K. 1975. Primary productivity of the Fraser River delta foreshore: yield estimates of emergent vegetation. M.Sc. thesis, Univ. British Columbia, Dept. Plant Sci. 134 p.

YUNG, K. Y. C. 1979. McGregor River diversion. Lower Fraser River — water level studies. Can. Soc. Civil Eng. 4th Nat. Hydrotech. Conf. River Basin Manage. p. 196–210.

ZARBOCK, W. M. 1977. Fish, fisheries and water quality of the Great Lakes basin. Fisheries. 2: 2–4, 26–33.

The Columbia River — Toward a Holistic Understanding

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Abstract

EBEL, J. W., C. D. BECKER, J. W.MULLAN, AND H. L. RAYMOND. 1989. The Columbia River — toward a holistic understanding, p. 205-219. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The Columbia River is one of the world's great rivers. It supports large runs of anadromous fish — several species of Pacific salmon and steelhead trout. Its watershed covers 671 000 km^2, including parts of British Columbia, Washington, Oregon, Idaho, Montana, and Wyoming, and the average annual flow rate at the river's outlet is about 6 655$m^3 \cdot s^{-1}$. Hydroelectric power, irrigation, and exploitation of regional resources other than water have greatly modified physical features throughout the Columbia River's vast system. Commercial and sport fishing, combined with alteration and degradation of riverine habitat, have reduced annual returns of anadromous fish from about 10 to 16 million originally to 2.5 million today. Efforts by management agencies to deal with the declines have focused on catch restriction, fish passage problems at dams, artificial propagation, habitat improvement, and identification of stocks at sea. Today, management is a joint effort by federal, regional, and state agencies and Indian tribes. Increased returns of anadromous fish to the river since 1980 are encouraging, but much remains to be done.

Résumé

EBEL, W. J., C. D. BECKER, J. W. MULLAN, AND H. L. RAYMOND. 1989. The Columbia River — toward a holistic understanding, p. 205–219. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Le Columbia est l'un des grands fleuves du monde. Il s'y fait d'importantes remontées anadromes (plusieurs espèces de saumons du Pacifique et la truite arc-en-ciel). Il a un bassin hydrologique de 671 000 km^2, qui recouvre des parties de la Colombie-Britannique et des États de Washington, de l'Orégon, de l'Idaho, du Montana, et du Wyoming; il a un débit annuel moyen de 6655 $m^3 \cdot s^{-1}$. Les ouvrages hydroélectriques, l'irrigation et l'exploitation des ressources régionales autres que l'eau ont profondément modifié les traits physiques dans l'ensemble de ce vaste bassin. Les pêches commerciales et sportives, en plus de la transformation et de la dégradation des habitats riverains, ont eu pour effet de réduire les remontées annuelles, de 10 à 16 millions à l'origine jusqu'à 2,5 millions aujourd'hui. En réaction, les organismes de réglementation ont fait porter leurs efforts sur les limites de capture, les problèmes de remonte aux barrages, la multiplication par des moyens artificiels, la remise en état de l'habitat et l'identification des stocks en mer. La gestion des stocks est devenue une entreprise conjointe où sont réunis les efforts des gouvernements fédéral et régionaux, des services d'États et des bandes indiennes. Les remontées plus abondantes dans le fleuve depuis 1980 sont encourageantes, mais il reste encore beaucoup de travail à faire.

Introduction

The Columbia River is one of the world's great rivers. It drains 671 000 km^2, (259 000 mi^2) and discharges over twice the amount of water as the Nile River in Egypt. The Columbia River also produces large runs of Pacific salmon (*Oncorhynchus* spp.) and steelhead trout (*Salmo gairdneri*), and has served as a focal point for the evolution of northwest native cultures dependent on these fish. The river's discovery in 1792 by Captain Robert Gray and its exploration in 1805 by Lewis and Clark set in motion changes that profoundly altered the river and its watershed.

The river's capacity for sustained production of salmonids was greatest prior to 1930. Before encroachment by white settlers, the aboriginal fishery was estimated to take about 8.2×10^6 kg (18 million lb) (Craig and Hacker 1950) or 11.3×10^6 kg (25 million lb) (Hewes 1972) of fish each year. During the peak period of commercial fishing (1916 to 1920), catches exceeded 18.1×10^6 kg (40 million lb) each year. Even today, with the runs depressed, the annual combined catch of commercial, sport, and tribal fisheries exceeds 9.1×10^6 kg (20 million lb).

In terms of numbers, salmon and steelhead runs ranged from about 10 to 16 million fish, annually before major development of the Columbia River Basin (Northwest Power Planning Council 1986). Current runs average about 2.5 million fish, indicating that basin-wide losses have been about 7 to 14 million fish. Chief Joseph Dam on the Columbia River and Hells Canyon Dam on a major tributary, the Snake River, blocked return runs, and eliminated all habitat for anadromous fish production above them. Declines in runs of anadromous fish have been greatest in the upper Columbia and Snake rivers because of habitat loss and mortalities of upstream and downstream migrants at dams.

The history of the Pacific Northwest is marked by conflicts among fishermen, and between fishermen and other users over control of the Columbia River. Overfishing and resource allocation have been continuing problems. Economic development has, over the years, degraded or eliminated habitat and thereby decreased the system's capacity to produce anadromous fish. Hydropower leads the list, but agriculture and irrigation, logging, mining, stream channelization and clearing, and water pollution have all altered the river's ecosystem.

In this report, we first describe the ecological features of the Columbia River. We then focus on the salmonid resources: commercial and sport fisheries, effects of regional development and exploitation, smolt passage problems, artificial propagation, and institutional arrangements for management. We review needs and opportunities related to salmonid production.

Morphometry

The Columbia River begins at Columbia Lake in the Canadian Rockies. The river flows northwesterly in British Columbia for about 306 km (190 mi), then south 436 km (271 mi) across the Okanogan Highlands to Trail, British Columbia. It continues south across the international border to receive the Spokane River, then curves westward over the semi-arid Columbia Plateau to receive the Snake River near the Washington/Oregon border. At this point, the river turns west and flows about 483 km (300 mi) through the Cascade and Coast ranges to enter the Pacific Ocean near Astoria, Oregon (Fig. 1).

From source to outlet, the Columbia River extends over 1930 km (1200 mi) and drops 808 m (2650 ft). It passes through four mountain ranges: the Rockies, Selkirks, Cascades, and Coast; traverses several climatic zones from alpine to shrub-steppe to coastal; and receives flows from several large tributaries before discharging to the sea. The Snake River, the largest tributary, extends 1671 km (1038 mi) and drains 49 % of the system's watershed in the United States.

The Cascade Range forms a mountainous barrier to the passage of moisture inland from the Pacific Ocean. East of the Cascades is an open landscape, the Columbia Plateau, which was formed over millions of years from discontinuous flows of lava that solidified as basalt in nearly horizontal layers. As a result, parts of the mainstem Columbia and Snake rivers are entrenched in spectacular gorges.

Hydrology

The Columbia's average annual flow rate at its outlet is about 6655 $m^3 \cdot s^{-1}$ (235 000 $ft^3 \cdot s^{-1}$). Discharges from the Snake River average about 1300 $m^3 \cdot s^{-1}$ (46 000 $ft^3 \cdot s^{-1}$) annually (Pacific Northwest Regional Commission 1979). Nearly 25 % of the Columbia's total runoff originates west of the Cascade Range, an area less than 10 % of the total drainage, because of its higher precipitation.

Major tributaries of the mainstem Columbia River are: the Kootenai and Pend Oreille rivers in Canada; the Spokane, Okanogan, Wenatchee, Yakima, Snake, Cowlitz, and Lewis rivers in Washington; and the Umatilla, John Day, Deschutes, and Willamette rivers in Oregon. The interior drainage area extends to Idaho, Montana, and Wyoming.

In general, tributaries of the Columbia River originate in high, forested mountains where the climate is mesic, the gradient is steep, stream velocity is high, and scouring occurs. In the Columbia Basin proper, the climate is xeric, the gradient is less steep, stream flow is reduced, and sediment is deposited seasonally. The Cascade Range near the river's mouth is forested and receives heavy rainfall.

The main factors influencing hydrographs of Columbia River tributaries are changes in seasonal runoff and irrigation withdrawals. Hydrographs of the mainstem are influenced primarily by storage and release of water from impoundments for hydroelectric power production.

Mainstem Flow Regimes

Spring flows in the Columbia River are triggered by snowmelt and rain in headwater areas. Precipitation, primarily in the form of snow, is greatest in winter, and runoff increases with snowmelt during spring and early summer. Most major floods on tributaries east of the Cascades result from rapid snowmelt. The most severe spates are often accentuated by heavy, warm rain or warm wind. Convective storms accompanied by intense rainfall may also cause local floods.

Before impoundment of the mainstem, estimated discharges at the river's outlet averaged 18 690 $m^3 \cdot s^{-1}$ (660 000 $ft^3 \cdot s^{-1}$) from May through July and 1980 $m^3 \cdot s^{-1}$ (70 000 $ft^3 \cdot s^{-1}$) from September through March (Hickson and Rodolf 1957). Today, flows throughout the Columbia's drainage area are influenced by water storage projects. by 1973, the combined storage of Mica, Duncan, Arrow, Albeni Falls, Libby, Hungry Horse, and Grand Coulee dams (Fig. 1) provided capacity to store over $43\ 200 \times 10^6 \cdot m^3$ of spring runoff for use later in the year when more electricity is needed. As a result, in most years,

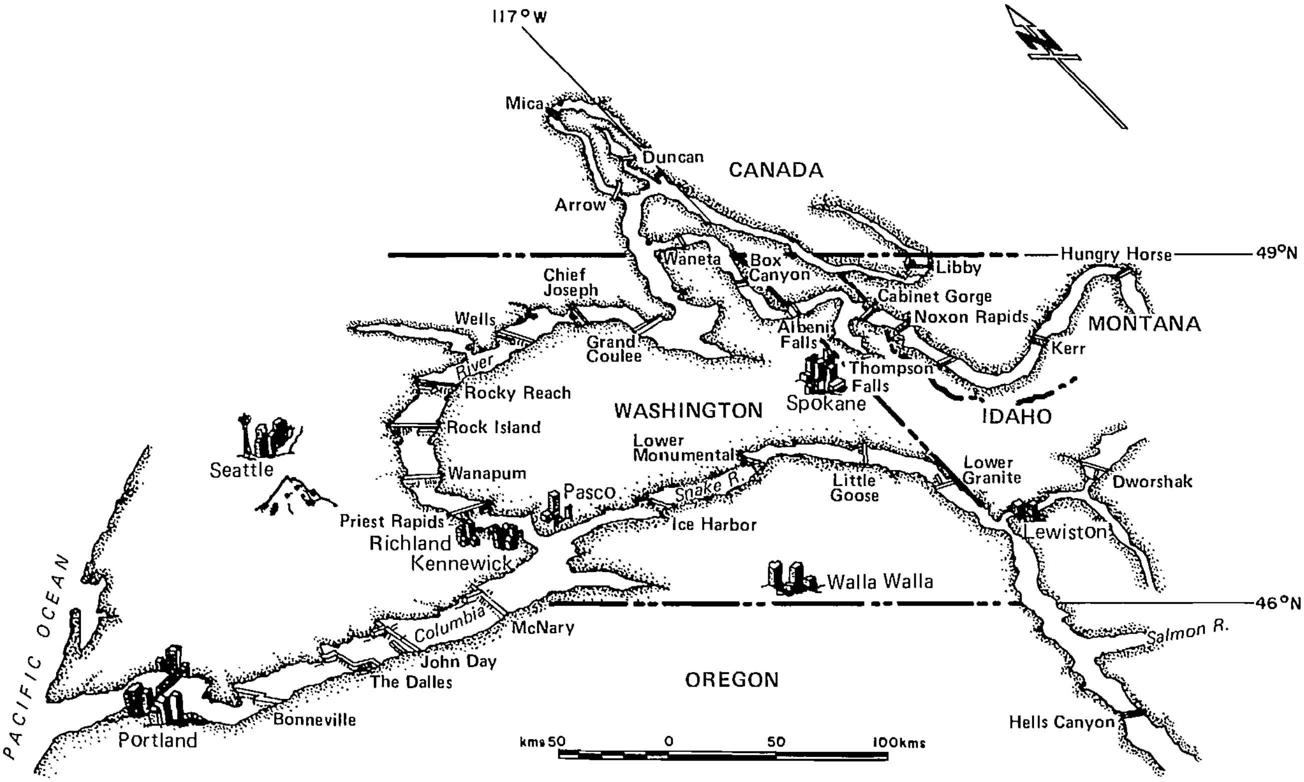

FIG. 1. The Columbia River system, showing the major tributaries, dams, and major metropolitan centers.

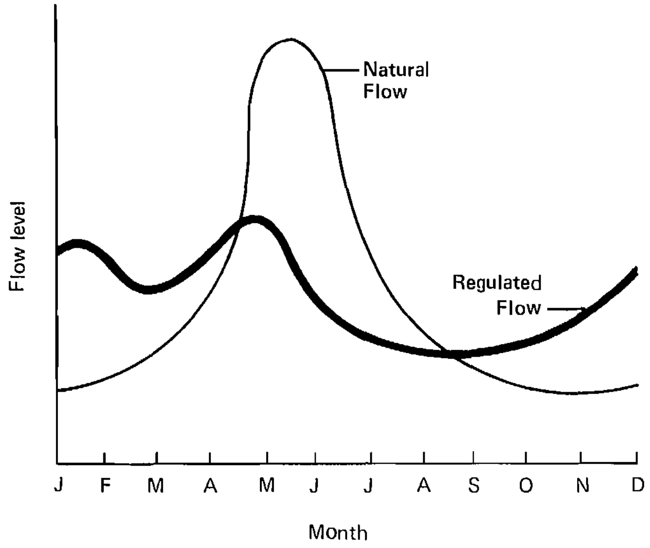

FIG. 2. Generalized effect of reservoir operations on mainstem Columbia River flows near The Dalles, Oregon. Tributary storage of water and mainstem production of hydropower eliminated the spring peak runoff that once transported juvenile salmonids downstream to the Pacific Ocean.

flows in the Columbia River when young salmonids migrate to sea in May and June have been reduced about 50% (Fig. 2). The system's total "active storage" capacity of 53 800 x $10^6 \cdot m^3$ represents about a quarter of the average annual runoff (Table 1).

Lake McNaughton of the Mica Project in Canada is the largest storage reservoir on the Columbia River system, and it may remain unfilled after seasonal drawdown. The Arrow Lakes in Canada are also used primarily for storage. Lake Roosevelt, behind Grand Coulee Dam, is the major storage reservoir in the United States; it contains 6400 x $10^6 \cdot m^3$) of active storage but has a total volume of 11 800 x $10^6 \cdot m^3$. Essentially, the whole mainstem below Lake Roosevelt is influenced by the storage and hydraulic capacities of Grand Coulee Dam.

The flushing rate of Lake Roosevelt is about 45 days. Below Grand Coulee Dam, flushing rates for river-run reservoirs vary from less than 1 day (Priest Rapids) to about 4 days (Lake Wallula). Current velocities in these impoundments average about 0.3 $m \cdot s^{-1}$. Lake Umatilla is primarily a storage reservoir, but it has a flushing rate of about 7 days.

Most storage reservoirs undergo major seasonal drawdown. For example, the elevation of Lake Roosevelt is lowered about 25 m (82 ft) each year prior to the spring spate (Stober et al. 1979). In contrast, water levels of most river-run reservoirs may fluctuate 0.3 to 1.5 m (1 to 5 ft) daily in response to power generation at their outlet dams.

The last unimpounded section of the mainstem of the Columbia River is the Hanford Reach, a 80.5 km (50 mi) section between the head of Lake Wallula and Priest Rapids Dam. It is not "free-flowing," but regulated by discharges at and above Priest Rapids Dam.

Discharge volumes from mainstem dams generally increase downstream. This is because of reduced reservoir storage ratios and increments of water from tributaries. Annual discharges at Bonneville Dam average near 164 000

TABLE 1. Storage characteristics of mainstem Columbia River reservoirs.

Dam	Reservoir (lake)	Location (RKM)	Length (km)	Total volume[a] $(\times 10^{6}\bullet m^{3})$	Mean annual discharge $(\times 10^{6}\bullet m^{3}\bullet {}^{-}yr^{-1})$	Storage ratio[b]	Flushing rate (days)[c]
Mica	McNaughton	1638	209	25 040	18 260	1.37	499
Revelstoke	—	1498	129	1 480	70 440	0.02	7.3
Keenleyside	Arrow	1255	216	9 250	35 775	0.26	94
Grand Coulee	F. D. Roosevelt	960	243	11 800	96 220	0.12	45
Chief Joseph	Rufus Woods	877	71	616	96 470	0.007	2.6
Wells	Pateros	830	45	370	100 420	0.004	—
Rocky Reach	Entiat	761	68	493	102 390	0.005	1.8
Rock Island	Rock Island	729	34	123	105 600	0.001	—
Wanapum	Wanapum	668	61	740	105 600	0.007	2.6
Priest Rapids	Priest Rapids	639	29	247	105 720	0.002	0.7
McNary	Wallula	470	98	1 727	150 995	0.011	4.0
John Day	Umatilla	348	122	3 084	153 960	0.020	7.3
The Dalles	Celilo	309	39	370	158 890	0.003	1.1
Bonneville	Bonneville	325	72	616	163 700	0.004	1.5

[a] Total volume (table data) represents the maximum capacity of water storage in a reservoir, and is significant ecologically. Active storage (text data) represents only the storage capacity sufficient to provide daily or weekly streamflow regulations.

[b] Storage ratio (annual) = $\frac{\text{Total volume}}{\text{Mean annual discharge rate}}$

This is also called the exchange rate or flushing rate, and has a value in years, convertible to days.

[c] Flushing rate = annual storage ratio × 365 (days). This is the number of days required, theoretically, to completely empty a reservoir at the mean annual discharge rate.

$\times 10^{6}\bullet m^{3}$. Also, reservoirs on the lower Columbia River are the widest and shallowest of the Columbia River system. The mean depth of Lake McNaughton near the river's origin is 58.5 m (192 ft), but Lake Bonneville near the river's outlet averages only 9 m (30 ft) deep. Flows below Bonneville Dam are under tidal influence.

Sedimentation

The drainage basin of the Columbia River contains a variety of igneous, metamorphic, and sedimentary rocks, as well as unconsolidated surficial deposits from ancient glaciers. Upstream, the sediments in Grand Coulee, Rocky Reach, Wanapum, and Priest Rapids reservoirs, are largely fine-grained, nonvolcanic, and carried in suspension (Whetten et al. 1969). Downstream, the sediments in Umatilla, Celilo, and Bonneville reservoirs are coarser, of andesitic volcanic origin, and make up most of the bedload. Erosion in the headwaters tends to be rapid because most andesitic formations are poorly consolidated and the local gradient is steep.

Amounts of suspended sediment in the mainstem of the Columbia river vary seasonally with input from tributaries, of which the Snake River is the greatest contributor. Most sediment is transported downstream during a few days or weeks of high spring discharge. During average or low flows, sediment is deposited in impoundments and slackwater areas. Much of this material is resuspended during high flows. Thus, maximum sediment loads enter the pacific Ocean during late spring and early summer, the period of maximum water discharge (Whetten et al. 1969).

Little sediment accumulates on the bed of the Columbia River except in slackwater areas and below Bonneville Dam. The river bed between reservoirs is either scoured to bedrock or covered with a thin deposit of coarse gravel. Bedload transport is evident only in the lower Columbia River and the amount transported is probably small, about 10 % of the total sediment load exclusive of dissolved materials (Whetten et al. 1969).

The Columbia River discharges about 10^{7} t of sediment each year (Nittrouer et al. 1979). However, fine sediment is not deposited to any extent in the Columbia River estuary. Substrate in the estuary consists of about 1 % gravel, 84 % sand, 13 % silt, and 2 % clay; silt accumulates in only about 10 % of the estuary (Hubbell et al. 1972). Beyond the estuary, bottom currents along the shore remain northward throughout the year. Thus, most sediment leaving the Columbia River is carried northward. Sand tends to accumulate nearshore at <60 m depth, and most silt settles on the midshelf at the 60- to 120-m depth (McManus 1972).

Water Quality

The State of Washington has designated the mainstem of the Columbia River as Class A, or excellent, for water quality standards. This designation means that the water is suitable for use by the public, industry, and agriculture; for rearing livestock, fish, and shellfish; and for wildlife habitat, recreation, and navigation.

Water in the Columbia River is a dilute calcium–magnesium, carbonate–bicarbonate type, with a total dissolved solids content of about 90 $mg\bullet L^{-1}$ (range 71 to 158 $mg\bullet L^{-1}$), from the international border downstream to the confluence with the Snake River. Tributaries that drain the eastern parts of the Columbia Plateau are more mineralized from extensive irrigation and the higher amounts of solutes available from semi-arid land. Consequently, moderately higher mineralization of the mainstem of the Columbia occurs below the outlet of the Snake River.

Water quality in some tributaries used extensively for irrigation may be degraded by return flows from agricultural lands. For example, the lower portion of the Yakima River is seasonally laden with nutrients, pesticides, and coliform bacteria, and reaches temperatures about 4°C above levels expected otherwise. The outlets of the Okanogan and Umatilla rivers show similar impairment (Stober et al. 1979).

Mainstem Temperatures

Temperatures in the Columbia River are lowest in January and February and highest in August and September. The river is warmest near its outlet, where temperatures usually peak near 21°C. Thermal regimes in tributaries throughout the drainage basin differ widely with location, elevation, and input from rainfall, snowmelt, glaciers, and aquifers.

Studies in the 1960's showed that the construction of river-run reservoirs on the mainstem of the Columbia River caused no significant changes in the average annual water temperature. However, storage and release of water from Lake Roosevelt had delayed the timing of peak summer temperatures below Grand Coulee Dam since 1941. This delay was about 30 days at Rock Island Dam and was reflected, to a lesser extent, as far downstream as Bonneville Dam near the river's outlet. Temperature extremes were moderated by the reservoir complex so that the river below Grand Coulee Dam today is slightly cooler in summer and slightly warmer in winter (Jaske and Goebel 1967; Jaske and Synoground 1970).

Historically, average temperatures at the mouth of the Snake River during August and September have always been a few degrees higher than those in the mainstem Columbia (Roebeck et al. 1954; Jaske and Synoground 1970). During late summer of some years, high water temperatures (20° to 22°C) and low dissolved oxygen levels ($<6 \text{ mg}\cdot\text{L}^{-1}$) make living conditions marginal for salmonids in lower Snake River reservoirs (Bennett et al. 1983).

Productive Potential

Reservoirs strongly affect energy dynamics in the mainstem of the Columbia River. Thermal stratification is restricted in river-run reservoirs, and their relatively high flushing rates limit primary productivity. Thermal stratification occurs seasonally in the lower end of Lake Roosevelt behind Grand Coulee Dam, which also has a definite density-flow regime (Jaske and Snyder 1967; Stober et al. 1977). The lower end of Brownlee Reservoir on the Snake River also stratifies thermally during the summer (Raleigh and Ebel 1968), but reservoirs on the lower Snake River merely develop thermal layering (Bennett et al. 1983).

Development of plankton populations in mainstem impoundments depends, among other things, on water retention in relation to seasonal temperatures. Density and stability of plankton are maximum in reservoirs with long retention times such as Lake Roosevelt and Brownlee Reservoir. Development of indigenous plankton populations in Rufus Woods Reservoir is limited by flushing times of less than four days (Erickson et al. 1977).

Primary Production

Allochthonous detritus is the main contributor of organic material in forested tributaries of the Columbia River. However, a proportionally large population of autochthonous primary producers occurs in the mainstem today. Primary producers in the mainstem of the Columbia River originate largely in reservoirs and are essentially transient, passing from one impoundment to the other at rates related to water retention times. In large part, lentic forms of primary producers pass downstream while periphytic forms are retained. Some periphyton are dislodged by fluctuations of water levels in reservoirs and in the Hanford Reach, and these also pass downstream.

The Upper Arrow, Lower Arrow, and McNaughton reservoirs in Canada are oligotrophic with dissolved oxygen near saturation at all depths. Nutrient levels are low, as is typical of oligotrophic lakes, and diatoms are the dominant phytoplankton. Thermal stratification in these lakes is limited and may not occur in most years (B.C. Research 1977).

Diatoms are predominant in reservoirs in the mainstem of the Columbia River below the international border. Abundance usually peaks in April to June, followed by a second, lesser peak in September to October. Average primary production during the growing season (May to October) in the forebay of Lake Roosevelt is 620 $\text{mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Stober et al. 1977). Carbon uptake values in the flowing Hanford Reach amount to 792 $\text{mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ during June and September, but drop to near zero during the winter (Neitzel et al. 1982a). Most phytoplankton (and zooplankton) in the Hanford Reach originate above Priest Rapids Dam and are in transit downstream.

Phosphate, nitrate, and silica concentrations in the mainstem show a definite seasonal change, peaking in the winter and falling in the summer. The summer minima are greatly affected by primary productivity. Near Clatskani, Oregon, below the city of Portland, the nitrate–phosphate ratio is 3:1 during the summer and 19:1 at other seasons (Park et al. 1970).

Zooplankton

Zooplankton reach peak abundance in reservoirs in the mainstem of the Columbia River from June to September, but densities are relatively low the rest of the year. The main zooplankton species are the cladocerans *Bosmina longirostris* and *Daphnia* spp., and the copepods *Cyclops bicuspidatus* and *Diaptomus ashlandi*.

Zooplankton densities peak near 50 000 (Earnest et al. 1966) and 60 000 $\text{organisms}\cdot\text{m}^{-3}$ (Stober at al. 1977) in Lake Roosevelt; 25 $195\cdot\text{m}^{-3}$ in Rufus Woods Reservoir (Erickson et al. 1977); $4500\cdot\text{m}^{-3}$ in the Hanford Reach (Neitzel et al. 1982b); and 12 $500\cdot\text{m}^{-3}$ in the lower Columbia River (Clark and Snyder 1970).

Secondary Production

Benthic communities in reservoirs in the mainstem of the Columbia River are dominated by populations of chironomids and oligochaetes (Stober et al. 1979; Beckman et al. 1985), but other benthic organisms may be abundant locally. The benthos is usually depleted in littoral zones where water levels fluctuate.

In the flowing Hanford Reach, caddisfly (Trichoptera) larvae (primarily *Hydropsyche cockerelli*), chironomid larvae, an encrusting sponge, annelids, and the crayfish

Pacifasticus leniusculus are common, but species diversity is low. Historically, the unimpounded Columbia River probably supported an average-to-rich bottom fauna in which caddisfly and chironomid larvae, mayfly nymphs, and molluscs predominated (Roebeck et al. 1954). Today, biomass estimates of benthic invertebrates in the Hanford Reach range from 6 to 237 $g \cdot m^{-2}$ during the winter period of maximum abundance (Beak Consultants, Inc. 1980).

General Productivity

The impounded Columbia River probably has greater primary productivity today than it did when still free-flowing. Mainstem reservoirs allow some development of plankton and periphyton populations, and additional nutrients are added from exogenous sources such as irrigation return water. Increased productive potential is paralleled by a general increase in the diversity and abundance of non-salmonid consumers in downstream impoundments (Mullan et al. 1986).

The period of highest primary productivity in mainstem Columbia River impoundments (June to September) may benefit juvenile salmonids that linger in them during outmigration. Some O-age chinook salmon (*0. tshawytscha*) now feed and grow in McNary, Umatilla, and John Day reservoirs (Miller and Sims 1984). The success of the fall chinook salmon population spawning in the Hanford Reach may depend, in part, on this enhancement to their nursery area.

Fish Species

At least 43 species of fish occur in the mid-Columbia River (Gray and Dauble 1977). While anadromous salmon and steelhead runs are the most important, the Columbia River has other valued fishery resources. Commercial species include the anadromous eulachon (*Thaleichthys pacificus*) and American shad (*Alosa sapidissima*), and a resident population of white sturgeon (*Acipenser transmontanus*). Sport catches include native salmonids such as cutthroat trout (*Salmo clarki*), rainbow trout, and mountain whitefish (*Prosopium williamsoni*), as well as introduced species such as largemouth (*Micropterus salmoides*) and smallmouth bass *M. dolomieui*), walleye (*Stizostedion vitreum*), yellow perch (*Perca flavescens*), crappie (*Pomoxis* spp.), and catfish (*Ictalurus* spp.).

Salmonid Resources of the Columbia River

The expanse of the Columbia River system and the anadromous life cycle of the Pacific salmons and steelhead trout tend.to mask direct cause-and-effect relationships. In some cases, even heavy harvest in the lower river and ocean did not reduce return runs until spawning and rearing habitats were lost and mortality of smolts passing downstream had increased. Adverse effects occurred in varying degrees over several years, and an observable impact on any particular stock did not appear until successive generations, years later. Further, many stocks spawned in widely separated areas, making discovery of low returns more difficult.

Inordinately broad space and time scales contributed, in part, to policital attitudes and laws promoting development of natural resources in the Columbia River Basin — of which water for irrigation and power was the most vital. The salmon and steelhead runs, and the people who depended on them, received little consideration until recent years. Today, anadromous salmonids, hydroelectric power generation, and resource developments in the Columbia River Basin are interrelated to an extent unequaled anywhere.

The following sections provide insight into fishery management problems. The effect of regional resource development on anadromous salmonids, and concurrent present and potential solutions to these problems are described.

Commercial and Sport Fisheries

Runs of salmon and steelhead to the Columbia River have declined over the years. Landings of chinook salmon, for which the Columbia River is most famous, reflect this trend. They show: (1) an estimated peak catch of 2.3 million fish (19.5×10^6 kg) in 1883, followed by a decline until 1889; (2) catches of around 1.5 million fish (11.3×10^6 kg) annually until 1920; and (3) a decline until 1959, with only about 0.3 million fish landed each year from 1960 to 1980, mostly fall chinook salmon (Fig. 3).

From the 1860's to 1900, commercial fisheries in the lower 322 km of the Columbia River concentrated on and soon depleted runs of high quality chinook salmon from the peak summer return. Catches then shifted to the early "spring" and later "fall" runs (Thompson 1951). Today, returns of chinook salmon to the Columbia River are still separated into distinct spring, summer, and fall runs.

As early as 1878, the Columbia River was closed to commercial fishing during March, April, late August, and early September. Resourceful fishermen soon discovered that salmon could be harvested by trolling in the ocean off the river's mouth. An estimated 500 boats were involved in the new troll fishery in 1915. By 1975, about 3300 troll vessels were licensed in Washington; 2000 in Oregon; 2500 in California; and 1400 in British Columbia. Then, as today, many trollers were licensed in more than one state or province, and made extended trips to other fishing areas. Also, the ability of trollers to catch salmon vastly improved as

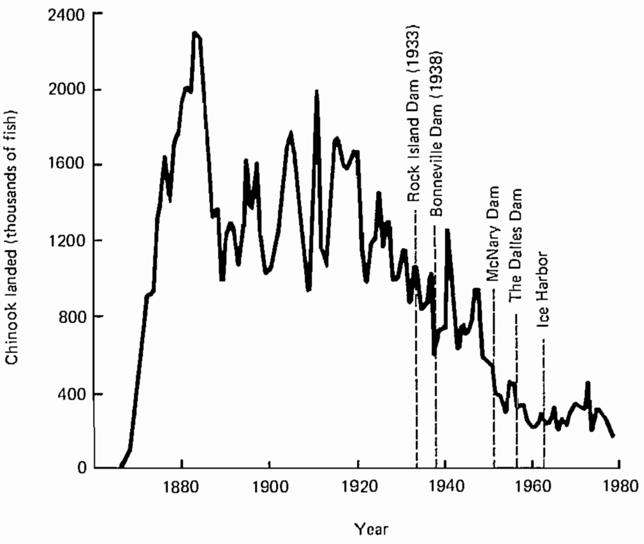

FIG. 3. Landing of chinook salmon by the Columbia River commercial fishery, 1866 to 1979 (from Chapman et al. 1982).

their range expanded and as gear efficiency improved.

Sport fisheries also expanded, albeit more slowly. By the late 1950's and 1960's, sport fishing became a major factor in reducing numbers of adult salmon and steelhead returning to the Columbia River.

Native Indian tribes have traditionally fished return runs in the mainstem Columbia River and various tributaries. Since 1979, certain treaty tribes have been legally entitled to 50 % of the allowable harvest. This fishery takes place primarily above Bonneville Dam.

By the early 1930's, the number of adult salmon and steelhead in the annual returns had fallen precipitously (Fig. 3). Concern for the fate of both fish and fishermen led to a patchwork of management organizations and a tangle of state regulations. The early organizations were ill-equipped to manage migratory fish that crossed and recrossed regulatory boundaries. At the same time, new problems arose as hydroelectric dams were built on the mainstem of the Columbia River. However, completion of Bonneville Dam on the lower Columbia River in 1938 gave management a new tool — they could now enumerate adult returns and obtain good estimates of escapement size for each species and run.

In retrospect, three factors contributed to reduced catches of chinook and coho (*O. kisutch*) salmon before 1960: (1) overfishing; (2) decreased production of juveniles, resulting from loss and degradation of spawning/rearing areas; and (3) mortalities of upstream and downstream migrants at dams. Also, hatcheries built prior to 1960 had limited success in compensating for reduced natural production.

Few data exist before the 1960's on the contribution of sport fishing to the total harvest. From this point, the rise in ocean sport catches reflected increased popularity and expansion of the fishery, and more extensive and successful hatchery operations (Chaney and Perry 1976). Sport fishermen caught nearly 500 000 coho salmon of Columbia River origin in 1971 and 200 000 chinook salmon in 1976. Most of these catches were fish of hatchery origin.

Today, salmonids from the Columbia River are caught in the ocean from Monterey, California, to southeastern Alaska. They range widely in the ocean and freely cross political boundaries. Thus, different runs are harvested according to their dispersal patterns. Fall chinook salmon from the lower Columbia River dominate the ocean troll catches from central Oregon to mid-Vancouver Island. Fall chinook salmon from the upper Columbia River migrate farther north and are harvested heavily in waters off British Columbia and Alaska. The chinook salmon from the depleted summer run generally move north (Chapman et al. 1982; Fraidenburg and Lincoln 1985). Spring chinook salmon from the upper Columbia River move north of the river's outlet, whereas those from the Snake River go both north and south (Wahle et al. 1981). Coho salmon from the lower Columbia River are caught mainly off the coasts of California, Oregon, and Washington. In contrast, sockeye salmon (*O. nerka*) and steelhead are not greatly exploited at sea.

Regulating the harvest of mixed stocks of salmonids in the ocean remains a major management problem. Identification of individual stocks or specific fish by stream of origin is difficult. When summer chinook salmon from the Salmon River, Idaho, reach the ocean, they intermingle with runs of summer, spring, and fall chinook salmon from different streams along the Pacific coast. The mixed stocks, each composed of several age groups, are harvested by fishermen from Alaska, British Columbia, Washington, Oregon, and California. Thus, fish from weak runs may be caught along with fish from strong runs--runs still abundant enough to support sport and commercial catches.

Regional Exploitation and Development

As the fisheries expanded, physical changes began to affect adversely salmonid populations of the Columbia River. Exploitation of natural resources proceeded rapidly after 1830, but substantial impacts on salmon runs were not clearly documented until after 1902. In that year, President Theodore Roosevelt's administration passed the Reclamation Act, which eventually led to 28 major reclamation projects.

Economic growth in the Columbia Basin was inevitable. Regional development eliminated or altered fish habitat, caused fish passage and pollution problems, and imposed major constraints on anadromous fish runs.

Dam Construction and Operation

Dams were built primarily for irrigation and power, but they also enhanced navigation, flood control, recreation, and industrial production. The Grand Coulee project on the Columbia River and the Brownlee project on the Snake River had major impacts on salmonid runs. Grand Coulee Dam, operational since 1941, was built without fish ladders and thus prevented access for anadromous fish to over 1100 miles of habitat in the upper Columbia River. Brownlee Dam, operational in 1958, terminated all fish passage to the upper Snake River. Overall, 22 dams were completed on the mainstem of the Snake and Columbia rivers by 1975 (Table 2). They blocked about 50 % of the inland headwaters from access by anadromous fish.

Wherever dams were installed, their impoundments inundated the spawning areas used by anadromous fish and significantly delayed the seaward migrations of smolts (Raymond 1979). Eventually, about 783 km (486 mi) of lotic river environment were converted into lentic or semilentic reservoirs.

TABLE 2. Mainstem dams adversely affecting anadromous fish runs on the Columbia and Snake river systems and their initial year of service.

Columbia River	Year of initial service	Snake River	Year of initial service
Rock Island	1933	Swan Falls	1910
Bonneville	1938	Lower Salmon Falls	1910
Grand Coulee	1941	Bliss	1949
McNary	1953	C.J. Strike	1952
Chief Joseph	1955	Brownlee	1958
The Dalles	1957	Oxbow	1961
Priest Rapids	1959	Ice Harbor	1961
Rocky Reach	1961	Hells Canyon	1967
Wanapum	1963	Lower Monumental	1969
Wells	1967	Little Goose	1970
John Day	1968	Lower Granite	1975

Reservoir habitats favor an increase in numbers of resident predator fish such as northern squawfish (*Ptychocheilus oregonensis*), largemouth and smallmouth bass, and walleye, all of which may prey on juvenile salmonids (Raymond 1979). Delays in downstream migration of smolts from the interconnected reservoir system can also extend their residence time and hinder osmoregulation on their entry to seawater (Adams et al. 1975; Zaugg and McLain 1972).

Mortalities of adult upstream and juvenile downstream migrants have caused great concern since the 1940's. Adult passage facilities at downstream dams were often ineffective, and delays were sometimes accompanied by adult mortality (Beiningen and Ebel 1970; Liscom et al. 1977; Johnson et al. 1982). Fishway designs were improved to attract and pass returning adults. Subsequent research showed that juvenile fish suffered high mortalities from passage through turbines at each dam, from predation on stressed fish below dams, and from delayed passage through consecutive reservoirs (Collins 1976; Ebel and Raymond 1976; Ebel et al. 1979; Raymond 1979).

Agriculture and Irrigation

Over 10 × 10^6 ha are used for agriculture in the Columbia Basin. Impacts on fish and fisheries arise primarily from water withdrawal, soil erosion and sedimentation, and from leaching of animal wastes, fertilizers, and pesticides to streams.

Early irrigation systems were unscreened and they entrained juvenile fish into canals and ditches to die. Today, most diversion intakes are screened on streams used by anadromous fish, but withdrawal of water still lowers flows on some tributaries to critically low levels, reducing or eliminating salmonid production.

The semi-arid ranges of the interior Columbia Basin were overgrazed from the time of early settlement. Uncontrolled grazing contributed to erosion and siltation of tributary streams. Grazing also destroyed riparian vegetation, and caused increases in water temperature and organic pollution. Overgrazing in riparian areas along tributaries remains a problem. Fish production in ungrazed streams is from 2.4 to 5 times higher than in grazed streams (Platts 1981).

Logging

Effects of logging include blockage to and alteration of stream habitat, sedimentation, and degradation of water quality through application of fertilizers, herbicides, and pesticides (NPPC 1986). The result is reduced productivity of tributary streams for salmonids.

Logging probably had its greatest impact from 1880 to 1910, especially in the Willamette River drainage, and in southwestern Washington where over 100 splash dams were built to transport logs downstream. The South Fork of the Salmon River, Idaho, was severely damaged between 1952 and 1965 when spawning gravels became heavily silted.

Mining

Mining activities in the Columbia Basin began early, particularly for gold and silver, and were extensive in the mid-1880's. Mining districts were formed and worked on the Salmon, Boise, John Day, Powder, Coeur d'Alene, and Clark Fork rivers (NPPC 1986). Placer mining, often by dredges, displaced stream gravel, added sediment downstream, and eliminated salmonids from many productive areas in Oregon and Idaho. Lode mining degraded water quality by seepage from tailing ponds and mines, especially in Idaho.

Stream Channelization and Clearing

Stream channelization and clearing degraded and destroyed salmon habitat in many streams. Waterways were initially highways for transport of settlers and supplies. The advent and use of the automobile in mountains required that roads be placed along waterways. Boulders and woody debris were often cleared from streams, and this material was used to dike off sloughs and side channels to consolidate the main stream. The cleanup of debris in hundreds of streams during the late 1940's and early 1950's is now viewed as misguided effort.

Industrial Pollution

The discharge of untreated wastes from municipal and industrial sources into Columbia Basin streams accompanied population growth in the 20th century. Effluents from sewage treatment plants, pulp and paper mills, and aluminum plants produced much of the pollution. Runoff from urban nonpoint sources also increased pollution loads (NPPC 1986).

By the 1960's, pollution in the lower Willamette River became so severe that oxygen levels were critically low (0–3 ppm), juvenile migrants attempting to reach the Columbia River suffered losses, and adults attempting to enter the Willamette River were delayed (Fish and Wagner 1950). Plutonium production reactors in the Hanford Reach from 1944 to 1971 used once-through cooling and released radioactivity and heat. However, effluent monitoring and onsite studies showed no effects on fish or other aquatic biota from radioactivity, and minimal to no effects from heated water. More recently, sublethal concentrations of fluoride ($0.3-0.5\ \mathrm{mg}\cdot\mathrm{L}^{-1}$) in effluents from an aluminum plant caused excessive delays of adult upstream migrants at John Day Dam (Damkaer and Dey 1985); fluoride discharges were reduced in 1983, and delays are no longer apparent.

Point-source discharges are not viewed as a serious problem in most of the Columbia River drainage today because the Clean Water Act of 1972 has legislated improved treatment of both industrial and municipal wastes, and point-source discharges are regulated by National Pollution Discharge Elimination System permits.

Smolt Passage Problems

Upriver stocks of salmon and steelhead in the Columbia River have been severely stressed because juveniles must pass eight or nine mainstem dams and reservoirs to reach the sea. Losses at each dam are substantial. From 1968 to 1975, when the four latest mainstem dams were completed on the Snake and Columbia rivers, average survival of juvenile spring chinook salmon passing from the upper Snake River to The Dalles Dam was reduced from 63 to

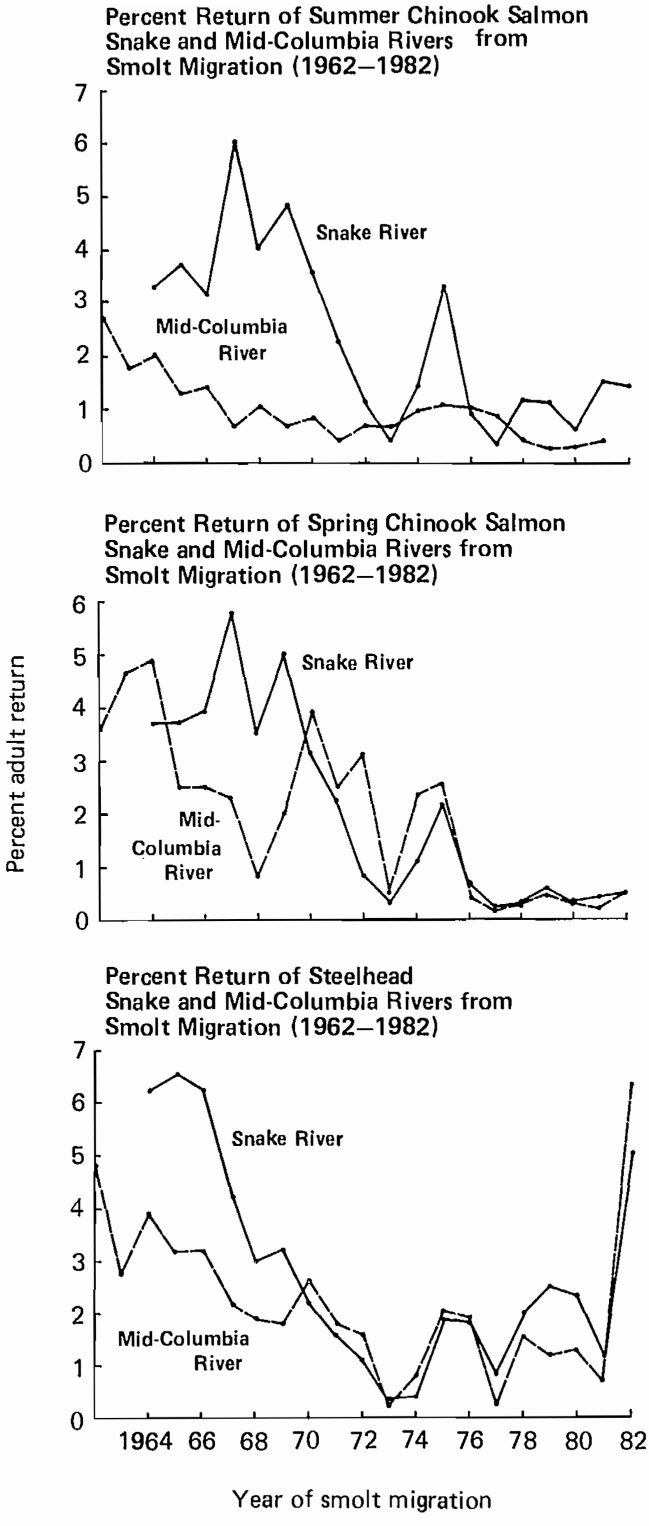

FIG. 4. Percentage return of chinook salmon and steelhead trout to the Snake River and mid-Columbia River dams based on smolt migrations during 1962 to 1982.

20 % (Raymond 1979).

In low flow years, most of the water is passed through turbines at dams, causing high mortalities of smolts from injury and, later, predation. Outmigrant losses range from 15 to 30 % at each dam, and cumulative losses during low water years are particularly severe (Ebel et al. 1979; NPPC 1986). During 1973 when flows were low, about 95 % of all juvenile salmon and steelhead emigrating from the Snake River were lost before they reached the Columbia River's estuary. By 1972, increased storage from the Mica and Arrow Lakes projects in Canada and increased turbine capacity of dams in the United States resulted in little or no spill at mainstem dams in average, as well as in low-flow years.

In high-flow years, when more water passes over spillways at dams, the river may entrain air in the plunge basin, leading to supersaturation and "gas bubble" disease among fish. During high-flow years from 1965 to 1975, mortalities ranged from 40 to 95 % of all outmigrants from the Snake River (Ebel 1971; Ebel and Raymond 1976). Losses of smolts from turbine passage and predation are minimal during high flows because most outmigrants pass with the spill and immediate mortalities are less than 3 % (Schoeneman et al. 1961). Thus, smolt losses at dams are usually lower in high-flow years than in low flow years.

Mortalities during smolt migration are reflected in low returns of spring and summer chinook salmon and steelhead to the Snake and mid-Columbia rivers (Fig. 4). Percentage returns declined between 1962 and 1974, when additional dams were constructed on the lower Snake River.

Actions taken to reduce smolt mortalities include: (1) installation of spillway deflectors (Fig. 5) at key dams, to reduce supersaturation of air in water; (2) installation of fingerling bypasses at dams, to direct smolts away from turbine intakes; (3) development of target flows, to provide more water during fish migrations; (4) implementation of annual spills at dams, to provide safe passage downriver; and (5) collection of smolts at upriver dams, for transport and release downstream below Bolleville Dam. In addition, hatchery production was increased to compensate for losses at dams.

In 1984, 90 % survival of outmigrants was set as a standard for each dam by the Northwest Power Planning Council. This standard can be met at most dams in most years without special spill. Yet cumulative mortality remains high today. Increasing smolt survival at each dam to 94 % in normal or high water years, and to 90 % in low-water years, would be a significant achievement.

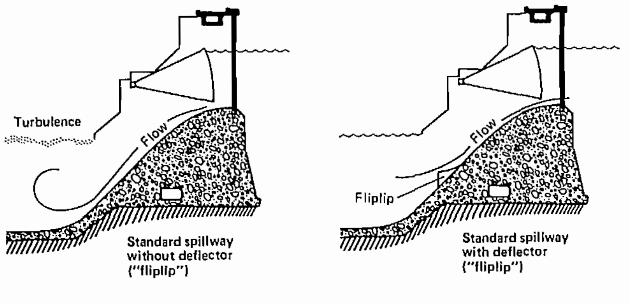

FIG. 5. Sketch of "Fliplip" deflector installed on spillways of Columbia River dams to reduce supersaturation of atmospheric gases.

Artificial Propagation

Compensation for losses of salmonids in the Columbia River system resulted in extensive rearing programs. By the late 1960's, hatchery production of fall chinook and coho salmon and steelhead far surpassed the remaining natural production. However, hatchery compensation is a two-edged sword. While releases supplement adult return runs, they also affect the survival of "wild runs." Large-scale production of hatchery fish on the lower Columbia River has been reported as detrimental to upriver runs of natural fish (NPPC 1986).

An estimated 395 million young salmonids weighing 3.0×10^6 kg (6.6×10^6 lb) were released in 1983 (GAIA Northwest Incorporated 1986). These fish were produced in 54 primary hatcheries or, including substations, 94 rearing facilities. Other hatcheries have begun operation since 1983. Thus, about 400 million anadromous fish are now stocked annually in the Columbia River system. The full potential of these hatcheries is near 1 billion smolts.

With such massive releases, hatchery salmonids now contribute substantially to catches of adult fish in the ocean and lower Columbia River. In 1977, about 75% of the coho salmon caught in ocean sport fisheries off the Oregon coast, and 85% of those caught off the Columbia River, came from hatcheries (Scarnecchia and Wagner 1979).

Young salmonids in hatcheries are not subject to high mortality in fresh water, as are naturally produced fish, because rearing conditions are controlled. Theoretically, hatchery stocks can withstand a greater harvest than natural stocks. While release of large numbers of fish from hatcheries as compensation for lost natural production did slow the decline of many runs, they also encouraged an increase in total harvest. Regulating mixed stocks for maximum allowable catches of hatchery fish caused the less productive natural stocks to erode (Lichatowich and McIntyre 1986). Further, it increased the dependence of many stocks on costly artificial propagation programs (PMFC 1982).

Institutional Arrangements

Until the early 1900's, anadromous fish in the Columbia River were harvested in estuaries and rivers as the adults returned to spawn. Initial effort to halt declines in the various runs was simply to restrict the commercial catch. Increasingly severe restrictions on inside fisheries failed to halt the downward trend. Analysis of the 1938 return runs led to the conclusions that the declines were caused primarily by overharvest (only 17% of the June–July chinook salmon run escaped to spawn), and that catch restrictions were limited by political infighting and, therefore, were largely ineffective (Rich 1941).

In subsequent years, the ocean fisheries expanded and more was learned about the behavior and migration of various species and stocks. Evidence now shows that protecting anadromous fish of the Columbia River requires regulation of catches in both fresh and salt water (Fig. 6). Early regulation of the ocean fishery was confined to seasonal catch restrictions, which were enforced by individual states with jurisdiction extending only 5.6 km (3 nmi) offshore. Federal jurisdiction was extended from 5.6 to 22.2 km (3 to 12 nmi) by passage of the Bartlett Act in 1966, and to 370.6 km (200 nmi) by the Fishery Conservation and Management Act in 1974. Further, early regulations were not always uniform among states and, generally, were not designed to achieve specific stock-by-stock escapement goals. Concepts of scientific fishery management did not begin to emerge until the 1940s.

In 1938, Congress passed the Mitchell Act authorizing

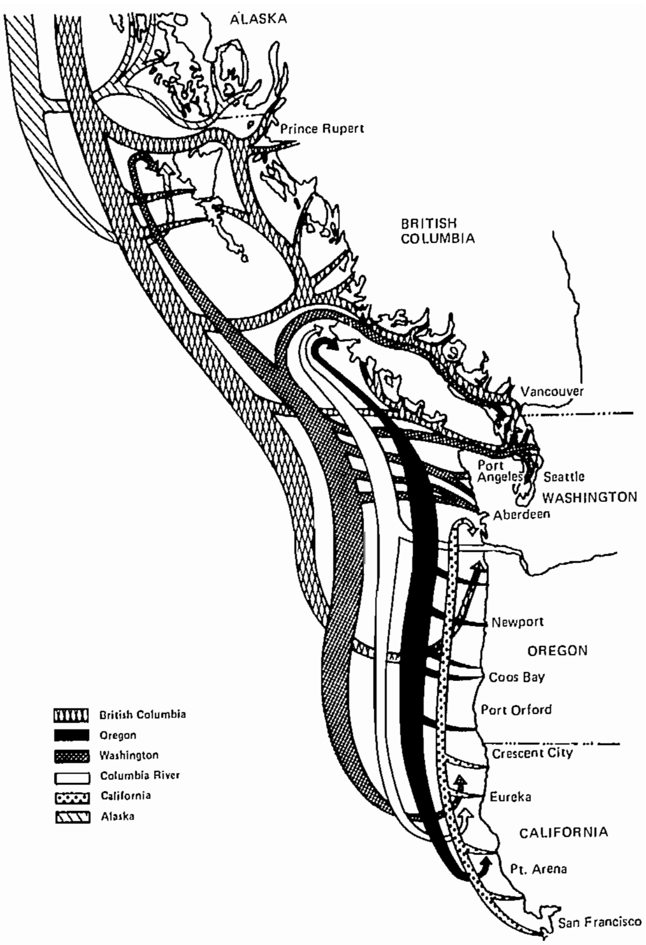

FIG. 6. General migration patterns of chinook salmon in northeastern Pacific Ocean. Migration patterns of coho salmon are similar.

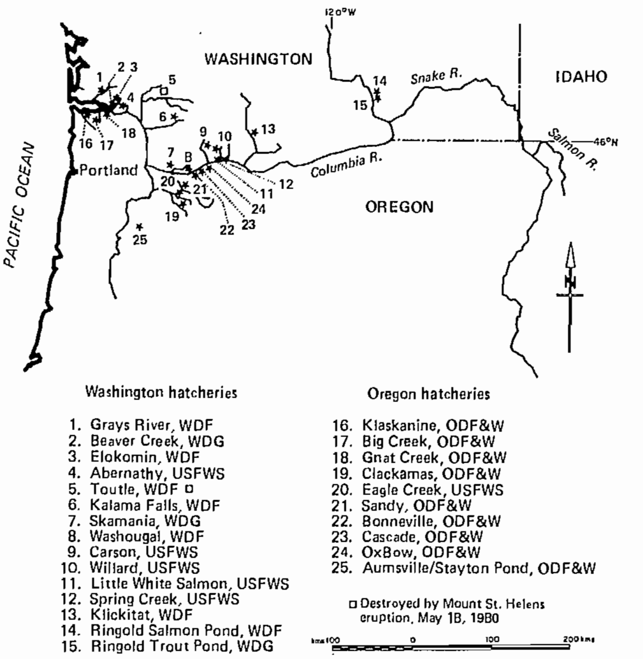

FIG. 7. Hatcheries funded under the Columbia River Fisheries Development program.

artificial propagation to compensate for destruction of habitat by hydroelectric development and other environmental changes. The Act was amended in 1946 to support state participation in stream improvement (fish passage over natural barriers, screening of irrigation diversions, and opening of streams blocked by debris), and in research to improve the quality of hatchery fish. Formalized as the Columbia River Fisheries Development Program, about 80 % of the available funds are now used to support 21 hatcheries and three rearing ponds (Fig. 7), with an annual production of about 100 million juvenile salmonids (Table 3).

Conflicts with various Indian tribes over regulation of tribal fisheries by states peaked in the early 1970's. These conflicts resulted in a 1979 ruling by the Supreme Court (the Boldt decision) that an 1855 treaty guaranteed 20 tribes the right to catch salmon and steelhead in their usual and accustomed places, and that the tribes were entitled to 50 % of the harvestable fish. Today, the treaty tribes participate in decisions affecting management of the resource through the Northwest Indian Fisheries Commission, the Columbia River Intertribal Fish Commission, and other liaison groups.

The federal government assumed management authority in 1974 with passage of the Fishery Conservation and Management Act. This Act established exclusive U.S. fishery authority over all salmon (and most other species) in the ocean within a 5.6–370.6 km (3–200 nmi) fishery conservation zone, except in territorial waters of other countries. Two regional councils for management were established under the Act: the Pacific Fisheries Management Council (PFMC) has jurisdiction off the coasts of California, Oregon, and Washington; the North Pacific Fishery Management Council (NPFMC) has jurisdiction off the coast of Alaska (Fig. 8).

The U.S./Canada salmon treaty, ratified in 1985, represented another milestone. It provided for regulating ocean fisheries to ensure meeting Indian treaty obligations, equitably distributing the catch between ocean and freshwater fisheries, and achieving spawning escapement goals (PMFC 1982).

With passage of the Water Resources Development Act of 1976, the Lower Snake River Fish and Wildlife Compensation Plan (SRCP) was authorized to compensate for losses of fish caused by hydroelectric projects on the Snake River. The SRCP called for hatchery releases sufficient to produce returns to the Snake River of 18 300 adult fall chinook salmon, 58 700 adult spring and summer chinook salmon, and 55 100 adult steelhead. Although such returns have not resulted to date, significant supplementation is occurring. The SRCP also called for release of 93 000 pounds of trout annually to compensate for loss of sport fish production in Washington and Idaho streams.

The Pacific Northwest Electric Power Planning and Conservation Act (NPCA) of 1980 and its accompanying Fish

TABLE 3. Numbers of salmonids released from hatcheries funded under the Columbia River Development Program from 1960 to 1984 (from Delarm and Wold 1985). All data × 10^6.

Year	Fall chinook salmon	Spring chinook salmon	Coho salmon	Steelhead trout	Totals
1960	89.1	1.8	6.4	1.0	98.3
1961	46.6	0.8	14.2	0.9	62.5
1962	55.8	1.7	12.9	1.6	72.0
1963	58.8	2.4	19.6	1.4	82.2
1964	65.5	7.6	16.5	1.7	91.3
1965	56.2	3.0	17.9	1.9	79.0
1966	54.9	3.8	19.7	2.5	80.9
1967	55.1	5.5	20.2	2.3	83.1
1968	55.5	3.8	15.7	3.0	78.0
1969	57.9	3.5	18.6	2.3	82.3
1970	62.2	2.6	17.4	2.9	85.1
1971	63.3	3.8	21.3	2.4	90.8
1972	67.1	3.6	23.9	2.5	97.1
1973	70.4	4.8	20.9	2.5	98.6
1974	65.5	4.4	20.2	2.3	92.4
1975	67.3	5.2	21.1	1.9	95.5
1976	84.0	5.9	22.2	2.1	114.2
1977	95.0	5.1	26.3	2.2	128.6
1978	89.3	5.5[a]	26.3	2.4	123.5
1979	89.1	7.5[a]	21.1	2.4	120.1
1980	80.1	7.2[a]	20.8	2.2	110.3
1981	73.3	7.6	19.2	2.3	102.4
1982	78.6	7.3	17.4	2.1	105.4
1983	74.5	6.9	21.7	2.1	105.2
1984	72.4	8.7	22.3	3.3	106.7

[a] Includes a small number of summer chinook salmon.

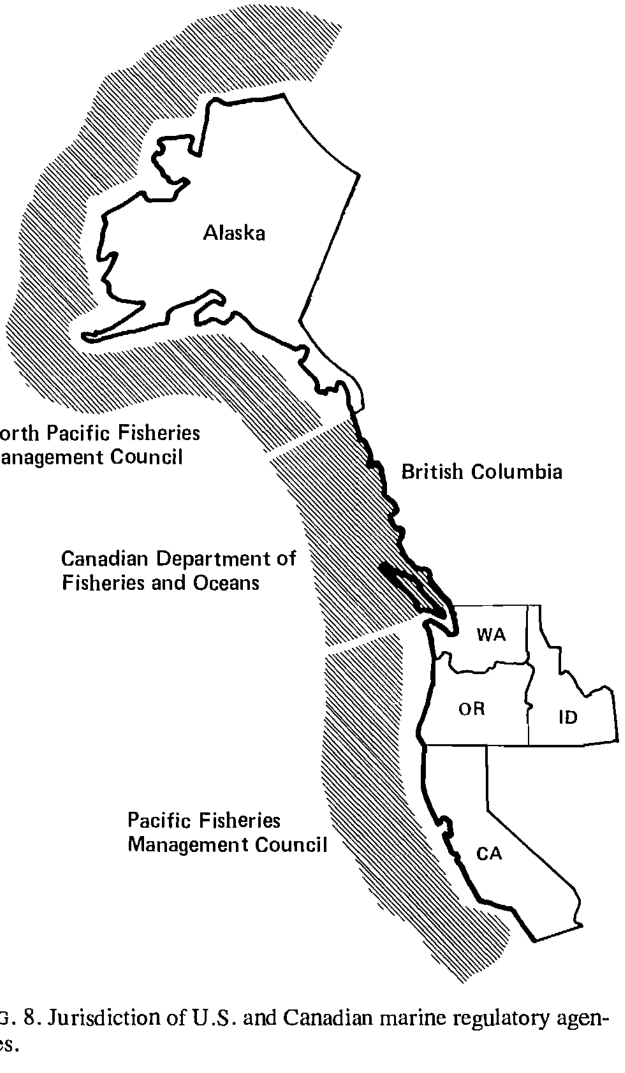

FIG. 8. Jurisdiction of U.S. and Canadian marine regulatory agencies.

and Wildlife Program (currently funded at about $30 million annually) represented another milestone, particularly in improving degraded habitat in the Columbia River. The Program includes a water budget that sets aside 5724 × $10^6 \cdot m^3$ of water each year to increase spills at dams from April 15 to June 15. Additionally, spill plans are drafted and implemented by fishery and tribal personnel working with public power utilities, the Corps of Engineers, and the Bonneville Power Administration. The intent is to reduce mortality of outmigrating smolts in turbines.

Public utilities and the Corps of Engineers have made substantial progress in compensating for salmon and steelhead losses at their dams on the Columbia River. Besides funding smolt production at hatcheries, they have spent millions of dollars annually to improve upstream and downstream passage of fish, and to provide adequate flows for fall chinook salmon spawning in the Hanford Reach below Priest Rapids Dam.

The results of these efforts are encouraging. Counts at Bonneville Dam since 1960 are listed in Table 4. About 440 000 salmonids were caught commercially in 1984. This was the highest catch since 1976 and may be attributed to a substantial increase in the size of runs.

Recent escapements are also encouraging. Several runs show an upward trend since 1980. Record returns of steelhead and fall chinook salmon in 1984 and 1985 reflect increased production of fall chinook salmon in the mid-Columbia River and benefits from improved passage of smolts. Upriver runs of summer chinook and sockeye salmon have also increased — this is especially evident from counts recorded in 1985.

Needs and Opportunities

The reasons that early efforts to compensate for declining salmon runs in the Columbia River were ineffective or failed include the unprecedented rate and magnitude of hydroelectric development on the Columbia River, and the limited knowledge and technology applicable to anadromous fish passage at the time. Many hatchery operations (e.g., hatcheries built to mitigate habitat loss from the Grand Coulee project) were conceived with inadequate background data as provisional experimental programs, subject to ongoing evaluation and updating, a proviso rarely done.

There was also the matter of priorities. Once dams were finished and operating, enthusiasm was often lost by construction agencies to see, and Congress to provide, compensation that was implied or promised when political support was sought for project appropriations. In addition, belated compensation programs were subjected to far more rigorous economic scrutiny than the projects that created the need (Chaney 1978). Nearly 15 years passed between completion by the Corps of Engineers of the first dam on the lower Snake River and the first compensation hatchery.

Numerous obstacles must still be faced to effectively manage anadromous salmonids of the Columbia River. New problems are likely to appear as greater insight is gained.

TABLE 4. Numbers of salmonids counted over Bonneville Dam on the lower Columbia River from 1960 to 1985.[a]

Year	Spring chinook salmon	Summer chinook salmon	Fall chinook salmon	Steelhead trout	Sockeye salmon	Coho salmon
1960	69 595	85 170	101 282	113 676	59 713	3 268
1961	98 695	66 461	119 916	139 719	17 111	3 456
1962	89 635	77 310	118 039	164 025	28 179	14 788
1963	75 473	64 013	139 079	129 418	60 319	12 658
1964	91 425	80 531	172 463	117 252	99 856	53 602
1965	84 261	75 974	157 685	166 453	55 125	76 032
1966	112 669	71 997	155 445	143 661	156 661	71 891
1967	84 935	95 659	185 643	121 872	144 158	96 488
1968	99 187	82 919	159 247	106 974	108 207	63 488
1969	173 566	102 153	231 838	140 782	59 636	49 378
1970	110 976	65 510	208 902	113 510	70 762	80 166
1971	125 517	77 911	202 274	193 966	87 447	75 989
1972	186 140	70 830	137 486	185 886	56 323	65 932
1973	142 148	45 360	211 127	157 823	58 979	54 609
1974	134 535	45 896	186 328	137 054	43 837	60 955
1975	104 104	44 351	277 111	85 540	58 212	58 307
1976	113 446	69 013	325 312	124 177	43 611	53 150
1977	119 508	41 023	206 126	193 437	99 829	19 408
1978	149 863	44 323	200 404	104 431	18 436	52 590
1979	51 462	34 217	190 613	113 979	52 628	45 328
1980	60 987	31 065	153 466	129 254	58 882	22 052
1981	65 009	26 929	193 712	159 270	56 037	30 510
1982	76 044	26 614	220 151	157 640	50 219	73 832
1983	56 838	23 458	164 180	213 779	100 527	15 176
1984	51 142	28 448	243 756	315 795	152 540	29 332
1985	90 964	29 353	334 436	326 194	165 928	55 529

[a] Dam counts indicate only escapement to the river, not total run size. Total run includes commercial and sport catches, and escapements to tributary streams below Bonneville Dam. Counts at dams today are further reduced by the Tribal fishery and a limited sport fishery above Bonneville Dam.

First, reducing smolt mortalities at dams remains an overwhelming need. Substantial progress has been made on developing and installing turbine screening and bypass systems at Columbia River dams. Yet technology still cannot reduce losses at each dam to less than 5% and few dams have yet attained such efficiency. Collection of seaward migrants in the Snake River at Lower Granite and Little Goose dams and at McNary Dam on the Columbia River, and barging or trucking them downstream, has produced favorable results. Steelhead and coho and fall chinook salmon have definitely benefited. The effectiveness of collection and transportation systems apparently varies with species, just as different abiotic factors influence losses at each dam.

Second, judicious allocation of spill over dams during seaward migration periods is required where effective turbine screen and bypass systems have not been installed. Not enough water is available in the mainstem of the Columbia and lower Snake rivers during years of low and average runoff for both hydroelectric power and downstream passage. The Water Budget of the NPPA Fish and Wildlife Program offers some improvement. Use of spill to reduce turbine mortalities may be an interim measure. Water for flushing smolts downstream and over dams will always be contested by other water users, particularly by power producers. The conflict emphasizes the need for adequate turbine screen and bypass systems.

Third, the problem of integrating hatchery releases and wild production without deleterious effects on wild stocks must be addressed. This includes density-dependent survival in fresh and salt water associated with large releases of smolts from hatcheries, and reduced survival of wild salmonids in tributaries laced with hatchery outplants to supplement natural spawning (Lichatowich and McIntyre 1986).

Fourth, disease continues to plague some hatchery stocks. Returns of upriver spring chinook salmon to federal hatcheries remain low. The presence of bacterial kidney disease (BKD) in hatchery stocks of spring chinook salmon that now contribute 70–80% of the seaward migration may cause poor survival (Banner et al. 1982; Fryer 1984). Juvenile spring chinook salmon are overwintered in hatcheries and released in early spring. Major BKD outbreaks occur near release time and may be induced by approaching smoltification. Could losses be reduced by new vaccines or by altering hatchery practices? Perhaps releases to impoundments in the fall for overwinter conditioning would increase survival.

Fifth, relationships between resident and migratory species need to be examined. Creation of impoundments and introduction of exotic fish has altered the composition and abundance of fish populations. Predation on salmonid outmigrants may be extensive, and other cause-and-effect relationships such as competition and disease transmission may exist.

Sixth, while pollution is not a major problem, information on current levels of contaminants in water, sediments, and fish tissue is incomplete. Salmonids in some areas now carry low burdens of polychlorinated biphenyls and chlorinated hydrocarbons, presumably derived from past industrial releases and return of contaminated irrigation water.

Seventh, mixed stock fisheries must be effectively regulated to prevent overharvest of wild stocks. This requires adequate data on the ocean distribution of stocks in the offshore fishery, the relative size of stocks available for harvest, and the response of stocks to oceanic conditions. Some data are available for hatchery fish from marking programs, but information on wild fish is meager. New techniques in stock identification (scale and parasite analysis, coded wire tags, genetic variant data) will help.

Eighth, efforts to increase natural production throughout the Columbia River system may be countered by construction of small hydropower dams on tributaries. The cumulative impact of hundreds of proposed projects on instream smolt production could be severe, depending on which projects are authorized.

According to one's philosophy, the resource base of salmon and steelhead in the Columbia River is either half empty (and declining) or half full (and increasing). The current program is not without critique (Anonymous 1986). However, the apparent success of recent management actions, which involve the cooperation of many agencies and governments, is encouraging. If current effort is continued, annual production of anadromous fish in the Columbia River system may increase to a level consistent with ecosystem changes and competing societal uses.

References

ADAMS, B. L., W. S. ZAUGG, AND L. R. MCLAIN. 1975. Inhibition of salt water survival and Na–K–ATPase elevation in steelhead trout (*Salmo gairdneri*) by moderate water temperatures. Trans. Am. Fish. Soc. 104: 766–769.

ANONYMOUS. 1986. The failed promise of the Columbia Basin Fish and Wildlife Program and what to do about it. Anadromous Fish Law Memo 38: 1–11.

BANNER, C. R., J. S. ROHOVEC, AND J. L. FRYER. 1982. *Renibacterium salmoninarum* as a cause of mortality among chinook salmon in saltwater, p. 236–239. *In* Proceedings, 14th Annual Meeting, World Mariculture Society.

BEAK CONSULTANTS, INC. 1980. Aquatic ecological studies near WNP-1, -2, and -4, August 1978–March 1980. WPPS Columbia River Ecology Studies, Vol. 7. Report to Washington State Public Power Supply System, Portland, OR.

B. C. RESEARCH. 1977. Limnology of Arrow, McNaughton, Upper Campbell, and Williston Lakes. Report for B. C. Hydro and Power Authority by Division of Applied Biology, B. C. Research, British Columbia, Canada.

BENNETT, D. H., P. M. BRATOVICK, W. KNOX, D. PALMER, AND H. ANSEL 1983. Status of the warmwater fishery and the potential of improving warmwater fishery habitat in lower Snake River reservoirs. Report to U.S. Army Corps of Engineers, Walla Walla District, by Dept. of Fish and Wildlife Resources, Univ. of Idaho, Moscow, ID. 451 p.

BECKMAN, L. G., J. F. NOVOTNY, W. R. PERSONS, AND T. T. TERRELL. 1985. Assessment of the fisheries and limnology in Lake F. D. Roosevelt, 1980–83. Report for U.S. Bureau of Reclamation by U.S. Fish and Wildlife Service, Natl. Fisheries Research Center, Seattle, WA. 168 p.

BEININGEN, K. T., AND W. J. EBEL. 1970. Effect of John Day Dam on dissolved nitrogen concentrations and salmon in the Columbia River, 1968. Trans. Am. Fish Soc. 99: 664–671.

CHANEY, E. 1978. A question of balance. Water/energy — salmon and steelhead production in the upper Columbia River Basin. Summary Report. Northwest Resource Information Center, Inc., 19 p.

CHANEY, E., AND L. E. PERRY. 1976. Columbia Basin salmon and steelhead analysis. Summary Report, Pacific Northwest Regional Commission. Portland, OR. 74 p.

CHAPMAN, D,. J. M. VAN HYNING AND D. H. MCKENZIE. 1982.

Alternative approaches to base run and compensation goals for Columbia River salmon and steelhead resources. Report to Chelan, Grant, and Douglas County PUDs by Pacific Northwest Laboratories, Richland, WA.

CLARK, S. M., AND G. R. SNYDER. 1970. Limnological study of lower Columbia River, 1967–1968. Spec. Sci. Rept. No. 610, U.S. Fish Wildl. Serv., Washington, DC.

COLLINS, G. B. 1976. Effects of dams on Pacific salmon and steelhead trout. Marine Fish. Rev. 38: 39–46.

CRAIG, J. A., AND R. L. HACKER. 1950. The history and development of the fisheries of the Columbia River. U.S. Bur. Commer. Fish., Bull. 49: 133–216.

DAMKAER, D. D., AND D. B. DEY. 1985. Effects of water-borne pollutants on salmon passage at John Day Dam, Columbia River (1982–1984). Northwest and Alaska Fish. Cent., Natl. Mar. Fish. Service, Seattle, WA.

DELARM, M. R., AND E. WOLD. 1985. Columbia River Fisheries Development Program. Annual Report for FY 1984. NOAA Technical Memo NMFS F/NWR-13. 42 p.

EARNEST, D. E., M. H. SPENSE, R. W. KISER, AND W. D. BRUNSON. 1966. A survey of the fish populations, zooplankton, bottom fauna, and some physical characteristics of Roosevelt Lake. Report to Washington Department of Game, Olympia, WA.

EBEL, W. J. 1971, Dissolved nitrogen concentrations in the Columbia and Snake Rivers in 1970 and their effect on chinook salmon and steelhead trout. NOAA Technical Report SSRF-646, Natl. Mar. Fish. Service, Seattle, WA.

EBEL, W. J. AND H. L. RAYMOND. 1976. Effect of atmospheric gas supersaturation on salmon and steelhead trout of the Snake and Columbia Rivers. Natl. Mar. Fish. Serv. Rev. 38: 1–14.

EBEL, W. J., G. K. TANONAKA, G. E. MONAN, H. L. RAYMOND, AND D. L. PARK. 1979. Status report — 1978; The Snake River salmon and steelhead crisis: Its relation to dams and the national energy shortage. NOAA Rept., Natl. Mar. Fish. Service, Seattle, WA 39 p.

ERICKSON, A. W., Q. J. STOBER, J. J. BRUEGGEMAN, AND R. L. KNIGHT. 1977. An assessment of the impact of the wildlife and fisheries resources of Rufus Woods Reservoir expected from the raising of Chief Joseph Dam from 946 to 956 ft m.s.l. Report to College Fisheries, Univ. of Washington, Seattle, WA.

FISH, F. F., AND R. A. WAGNER. 1950. Oxygen block in the mainstem Willamette River. Special Report, Fisheries No. 41. U.S. Fish Wildl. Serv. 19 p.

FRAIDENBURG, M. E., AND R. H. LINCOLN 1985. Wild chinook salmon management: an international conservation challenge. N. Am. J. Fish. Mgt. 5: 311–329.

FRYER, J. L. 1984. Epidemiology and control of infectious diseases of salmonids in the Columbia River Basin. Annual Report FY 1983. Project No. 83-312, Bonneville Power Administration, Portland, OR. 68 p.

GAIA NORTHWEST INCORPORATED (GAIA). 1986. Survey of artificial production of anadromous salmonids in the Columbia River Basin. Project 84-51, Bonneville Power Administration, Division of Fish and Wildlife, Portland, OR.

GRAY, R. J., AND D. D. DAUBLE. 1977. Checklist and relative abundance of fish species from the Hanford Reach of the Columbia River. Northwest Sci. 51: 208–215.

HEWES, G. W. 1972. Indian fisheries productivity in precontact times in the Pacific salmon area. Northwest Anthop. Res. Notes 7: 133–155.

HICKSON, R. E., AND F. W. RODOLF. 1957. History of the Columbia river jetties, p. 283–298. *In* Proceedings of the First Conference on Coastal Engineering, Council on Wave Research, the Engineering Foundation.

HUBBELL, D. W., J. L. GLENN, AND H. H. STEVENS, JR. 1972. Studies of sediment transport in the Columbia River estuary, p. 190–226. *In* Proceedings, 1971 Technical Conference on Estuaries in the Pacific Northwest, Circ. No. 42, Oregon State University Eng. Expt. Station, Corvallis, OR.

JASKE, R. T., AND J. B. GOEBEL. 1967. Effects of dam construction on temperatures of Columbia River. J. Am. Water Works Assoc. 59: 935–942.

JASKE, R. T., AND G. R. SNYDER. 1967. Density flow regime of Franklin D. Roosevelt Lake. J. Sanitary Eng. Div., Proc. Amer. Soc. Civil Eng. 93: 15–28.

JASKE, R. T., AND M. O. SNYOGROUND. 1970. Effect of Hanford plant operations on temperature of the Colummbia River, 1964 to present. BNWL-1345, Pacific Northwest Laboratory, Richland, WA.

JOHNSON, G. A., J. R. KUSKIE, JR., AND W. NAGY. 1982. The John Day Dam powerhouse adult fish collection system evaluation, 1979–80. Report, Portland District, U.S. Corps of Engineers, Bonneville Lock and Dam, Cascade Locks, OR. 175 p.

LICHATOWICH, J. A., AND J. D. MCINTYRE. 1986. Hatcheries and anadromous fish management. *In* Common Strategies of Anadromous and Catadromous Fish, An International Symposium. March 9–13, 1986. Boston, MA.

LISCOM, K. L., G. E. MONAN, AND L. C. STUEHRENBERG. 1977. Radio tracking studies of spring chinook salmon in relation to evaluating potential solutions to the fallback problem and increasing the effectiveness of the powerhouse collection system at Bonneville Dam, 1976. NOAA, Natl. Mar. Fish. Service, Seattle, WA. 32 p.

MCMANUS, D. A. 1972. Bottom topography and sediment texture near the Columbia River mouth, p. 241–253. *In* A. T. Pruter and D. L. Alverson [ed.] The Columbia River Estuary and Adjacent Waters. Univ. Washington Press, Seattle, WA.

MILLER, D. R., AND C. W. SIMS. 1984. Effects of flow on migratory behaviour and survival of juvenile fall and summer chinook salmon in John Day Reservoir. Annual Report of Research (FY 1983), NOAA, Natl. Mar. Fish. Service, Seattle, WA..

MULLAN, J. W., M. B. DELL, S. G. HAYS, AND J. A. MCGEE. 1986. Some factors affecting fish production in the mid-Columbia River 1934–1983. Report No. FRI/FAO-86-15, U.S. Fish and Wildl. Service, Seattle, WA. 69 p.

NEITZEL, D. A., T. L. PAGE, AND R. W. HANF, JR. 1982a. Mid-Columbia River microflora. J. Freshwater Ecol. 1: 495–505.

1982b. Mid-Columbia River zooplankton. Northwest Sci. 57: 112–118.

NITTROUER, C. A., R. W. STERNBERG, AND D. A. MCMANUS. 1979. Sedimentation on the Washington continental shelf. *In* W. E. Pequegnat and R. Darnell [ed.] The Ecology and Management of the Continental Shelf. Gulf. Publ. Co., Houston, TX.

NORTHWEST POWER PLANNING COUNCIL (NPPC). 1986. Compilation of information on salmon and steelhead losses in the Columbia River Basin. Columbia River basin Fish and Wildlife Program, NPPC, Portland, OR. 161 p.

PACIFIC MARINE FISHERIES COMMISSION (PMFC). 1982. Perspective on management of ocean chinook salmon fisheries within the fishery conservation zone of California, Oregon, and Washington. Pacific Fishery Management Council, Portland, OR. 25 p.

PACIFIC NORTHWEST REGIONAL COMMISSION (PNRC). 1979. Water Today and Tomorrow, Volume II, the Region. PNRC, Vancouver, WA.

PARK, P. K., M. CATALFOMO, G. W. WEBSTER, AND B. H. REID. 1970. Nutrients and carbon dioxide in the Columbia River. Limnol. Oceanogr. 15: 70–79.

PLATTS, W. S. 1981. Influence of forest and rangeland management on anadromous fish habitat in western North America — No. 7. Effects of livestock grazing. *In* General Technical Report, PNW-124. U.S. Dept. Agriculture, Pacific Northwest Forest and Range Experiment Station, Boise, ID. 25 p.

RALEIGH, R. F AND W. J. EBEL. 1968. Effect of Brownlee Reservoir on migrations of anadromous salmonids, p. 415-443. *In* Reservoir Fishery Resources Symposium, Athens, GA.

RAYMOND, H. L. 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966-1975. Trans. Am. Fish. Soc. 108: 505-529.

RICH, W. H. 1941. The present state of the Columbia River salmon resources. Fish Commission of Oregon, Contribution No. 3, Salem, OR. 6 p.

ROEBECK, G. G., C. HENDERSON, AND R. C. PALANGE. 1954. Water Quality Studies on the Columbia River. Special Report, Dept. of Health, Education and Welfare, U.S. Public Health Service, Washington, DC.

SCARNECCHIA, D. L., AND H. H. WAGNER. 1979. Contribution of wild and hatchery-reared coho salmon, *Oncorhynchus kisutch*, to the Oregon ocean sport fishery. Fish. Bull. 3: 617-623.

SCHOENEMAN, D. E., R. T. PRESSEY, AND C. O. JUNGE, JR. 1961. Mortalities of downstream migrant salmon at McNary Dam. Trans. Am. Fish. Soc. 90: 58-72.

STOBER, Q. J., R. W. TYLER, C. E. PETROSKY, T. J. CARLSON, D. GAUDET, AND R. E. NAKATANI. 1977. Survey of fishery resources in the forebay of Franklin D. Roosevelt Reservoir, 1976-77. FRI-UW-7724, Report to Bureau of Reclamation by Fisheries Research Institute, Univ. of Washington, Seattle, WA.

STOBER, Q. J., M. R. GRIBEN, R. V. WALKER, A. L. SETTER, I. NELSON, J. C. GISLASON, R. W. TYLER, AND E. O. SAIO. 1979. Columbia River Irrigation Withdrawal Environmental Review: Columbia River Fishery Study. FRI-UW-7919, Report to Portland District, U.S. Army Corps of Engineers, by Fisheries Research Institute, Univ. of Washington, Seattle, WA.

THOMPSON, W. F. 1951. An outline for salmon research in Alaska. Circular No. 18, Fisheries Research institute, Univ. of Washington, Seattle, WA.

WAHLE, R. J., E. C. HANEY, AND R. E. PEARSON. 1981. Aereal distribution of marked Columbia River basin spring chinook salmon recovered in fisheries and at parent hatcheries. Mar. Fish. Rev. 43: 1-9.

WHETTEN, J. T., J. C. KELLY, AND L. G. HANSON. 1969. Characteristics of Columbia River sediment and sediment transport. J. Sediment. Petrol. 39: 1149-1166.

ZAUGG, W. W., AND L. R. MCLAIN. 1972. Changes in gill adenosinetriphosphatase activity associated with parr-smolt transformation on steelhead trout, coho, and spring chinook salmon. J. Fish. Res. Board Can. 29: 167-171.

The Colorado River: Lifeline of the American Southwest[1]

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Abstract

CARLSON, C. A., AND R. T. MUTH. 1989. The Colorado River: lifeline of the American Southwest, p. 220–239. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

In less than a century, the wild Colorado River has been drastically and irreversibly transformed into a tamed, man-made system of regulated segments. The pristine Colorado, characterized by widely fluctuating flows and physico-chemical extremes, supported unique assemblages of indigenous flora and fauna. Closure of Hoover Dam in 1935 marked the end of the free-flowing river. The system has since become one of the most altered and intensively controlled in the United States; many mainstem and tributary dams, water diversions, and channelized river sections now exist in the basin. Despite having one of the most arid drainages in the world, the river supplies more water for consumptive use than any river in the United States. Its biota is dominated by non-native organisms, and about one third of its native fishes are threatened, endangered, or extinct. This paper treats the Colorado River holistically as an ecosystem and summarizes current knowledge on its ecology and management. Little has been published on productivity and fisheries of the mainstream river.

Résumé

CARLSON, C. A., AND R. T. MUTH. 1989. The Colorado River: lifeline of the American Southwest, p. 220–239. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

En moins d'un siècle, le cours sauvage du Colorado a été irrévocablement et très fortement modifié en un système artificiel de tronçons à débit régularisé. À son état vierge, le Colorado abritait des assemblages uniques d'animaux et de plantes indigènes; on y observait des fluctuations importantes du débit et des facteurs physico-chimiques. Depuis l'achèvement en 1935 du barrage Hoover qui a marqué la fin de l'état sauvage du fleuve, le système est devenu l'un des cours d'eau les plus perturbés et intensivement harnachés des États-Unis. Il existe maintenant dans le bassin versant de nombreux barrages, ouvrages de déviation et tronçons canalisés dans le tronçon principal et les tributaires. Malgré que son bassin hydrographique soit l'un des plus arides du globe, le Colorado fournit un plus grand volume d'eau à des fins de consommation que tout autre cours d'eau américain. Son biote est composé en grande partie d'organismes exotiques et environ un tiers de sa faune piscicole indigène est menacée, en danger de disparition ou disparue. On présente une vue globale du Colorado à titre d'écosystème et on résume les connaissances actuelles sur son écologie et sa gestion. Peu de données ont été publiées sur la productivité et les pêcheries dans le tronçon principal.

Introduction

"In a little over two generations, the wild Colorado has been harnessed by a series of dams strung like beads on a thread from the Gulf of California to the mountains of Wyoming. The living river that Powell knew has been sectioned into placid desert lakes throughout much of its length, and the river's primordial task of carrying the *massif* of the Colorado Plateau to the sea, bit by grainy bit, has been interrupted, and will remain interrupted for the lifetimes of our children's children and beyond." — Watkins (1969).

Despite years of study, the Colorado River has rarely been viewed holistically as an ecosystem (sensu Minshall et al. 1985), and much information on its biota is available only in the "gray" literature. This case history is intended to introduce the reader to the Colorado River System, with emphasis on current literature, including recent reviews by Graf (1985) and Stanford and Ward (1986a, 1986b, 1986c). We have drawn upon only the most significant elements of the extensive non-peer-reviewed literature.

Description of the Basin

The Colorado heads on the Never Summer Range in Rocky Mountain National Park, Colorado, and flows 2 320 km to the Gulf of California in Mexico (Fig. 1). The Green River, which joins the Colorado in Canyonlands National Park, Utah, originates in the Wind River Range of

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[1] Contribution 33, Colorado State University Larval Fish Laboratory.

FIG. 1. The Colorado River Basin (redrawn from Hely 1969 and Fradkin 1981).

southwestern Wyoming, 2 735 km from the Gulf of California.

The Colorado River Basin encompasses 632 000 km^2 in the United States and Mexico (Plummer 1983) and ranges in elevation from sea level to above 4 000 m (Carlson and Carlson 1982). It occupies one-twelfth of the land area of the contiguous United States and is divided into upper and lower basins for water management purposes. Sub-basins and conditions in the basin were reviewed by LaRue (1916), Sykes (1937), Iorns et al. (1965), Bishop and Porcella (1980), Carlson and Carlson (1982), Graf (1985), and Stanford and Ward (1986a).

The Colorado River drainage spans three geologic provinces: Rocky Mountains, Colorado Plateau, and Basin and Range (Hunt 1974). Igneous and metamorphic rock underlie headwater regions, but the river contacts marine deposits containing salts and fine-grained sediments downstream (Miller et al. 1983). Major geologic strata were summarized by Stanford and Ward (1986a). Various portions of the river system originated from 3.3 to over 20 million years ago (Minckley et al. 1986).

Human occupation of the Colorado River Basin dates to some of the earliest records of man as a nomadic hunter in the Western Hemisphere over 10 000 yr ago. Agricultural Anasazi, Fremont, Mogollon, and Hohokam cultures flourished at various times into the 1200s, creating extensive irrigation systems (Masse 1981) and exploiting fishes and game along watercourses (Bolton 1919). They declined and were succeeded by their descendants (Hopi, Taos, Zuni, and Pima-Papago) and immigrant Navaho, Apache, Southern Paiute, Havasupai, and Hualapai people (Watkins 1969; Fradkin 1981; Graf 1985). Spanish explorers in search of riches encountered the lower Colorado River in 1540 (LaRue 1916). The river was given several names before Father Kino applied the name 'Colorado' on a 1705 map of his passage westward in search of religious converts (Bolton 1919; Hughes 1967). White trappers continued exploration of the canyon country in the early 1800s, and William Ashley's party first navigated the upper Green River in 1825 (LaRue 1916; Watkins 1969). Mormon colonizers established towns along the river, and John Lee was sent by church leaders to establish a crossing below Glen Canyon (Fradkin 1981). Lee's ferry site has played a prominent role in the law of the river. John Wesley Powell's scientific investigations of the Colorado began in 1869, when he floated from Green River, Wyoming, through the Grand Canyon (Stegner 1982). Watkins (1969) and Fradkin (1981) have contributed excellent comprehensive reviews of subsequent Colorado River history. The first high dam on the mainstream river (Hoover Dam) was closed in 1935, marking the free-flowing Colorado's demise (Stanford and Ward 1986a). In the remainder of this paper, we summarize the status of the Colorado River ecosystem prior to 1935, briefly describe human manipulation of the basin's waterways, and assess the current condition and future of the river system and its biota.

The Colorado River before 1935

Prior to 1935, the river flowed essentially unchecked from its sources to the sea, ending in a "live delta" of meandering streams, silt, and shifting land patterns (Hundley 1966). Then, as now, much of its basin consisted of relatively barren deserts. High relief, sparse vegetation, and desert storms combined with montane snowmelt to produce spectacular variations in discharge (Minckley 1979; Table 1). The upper basin produced most of the river's discharge, and peak flows occurred after snowmelt in spring and early summer (Bishop and Porcella 1980). Maximum runoff in the lower basin often followed winter rainstorms (Sykes 1937). Lowest discharge typically occurred in mid to late summer, but long periods of low flows accompanied droughts.

At times of moderate flows and during droughts, the river ran clear, but sediment transport was remarkably high during floods. In high-gradient reaches, alluvial rubble from side channels resulted in formation of rapids between long, sand-bottom pools (Stanford and Ward 1986a). Unstable flows and other conditions resulted in arroyo cutting in small and medium-sized streams, and floods and droughts resulted, over time, in alternating braided and meandering channels (Graf 1985). Oxbow lakes and extensive, transitory marshes formed where the lower river occupied broad valleys. Minckley (1979) characterized the lower Colorado before regulation as "a broad, meandering, sandy-bottomed, periodically erosive, yet often aggrading stream".

TABLE 1. Selected physicochemical characteristics of the Colorado River before 1935 (Deacon and Minckley 1974; Dolan et al. 1974; US Geological Survey 1975; Weatherford and Jacoby 1975; Pillsbury 1981; Graf 1985; Stanford and Ward 1986a).

Discharge, range at Yuma, AZ	0 to 7 000 $m^3 \cdot s^{-1}$
Virgin flow, long-term annual mean from upper basin	16.65 km^3
Sediment transport, daily maximum in Grand Canyon	$25 \cdot 10^6$t
Seasonal water temperature ranges:	
Headwaters	0-20°C
Low-elevation desert streams	5->30°C
TDS:	
Headwaters	>50 $mg \cdot L^{-1}$
Lower mainstream	250–380 $mg \cdot L^{-1}$

Water temperatures in the pristine Colorado River probably resembled those recorded today in reaches far from mainstream reservoirs, and wide diurnal fluctuations were common (Minckley 1979). Chemical conditions before 1935 must have been almost as variable as discharge. Dissolved solids (TDS) concentrations differed with the geology of various sub-basins, but calcium, sulphate, and bicarbonate were predominant ions (Stanford and Ward 1986a). Local oxygen depletions probably were common in deeper backwaters along the lower river (Minckley 1979).

The biota of the Colorado River before 1935 is generally poorly documented. Headwater streams probably harbored plant and invertebrate communities like those currently present. Riverine algae were diverse but sparse, and nutrient levels were adequate to support considerable primary production during clear flows (Stanford and Ward 1986a). Autochthonous production was probably particularly important in areas on the lower river where marshy backwaters and oxbow lakes provided plant production that supplied organic detritus (Minkley 1979). Ward et al. (1986) stated that a highly adapted riverine zoobenthos existed at potamon sites in the upper basin but not in the Lower Mainstem Colorado. The trophic structure of the lower river probably was direct and simple. Chironomids and oligochaetes were the predominant benthic organisms. Only soft bottoms of backwaters and woody debris in main channels could have supported diverse and abundant invertebrate communities.

The Colorado River Basin has an unique indigenous fish fauna. The drainage was established long ago and has had no major connections with surrounding river basins for millions of years (Behnke and Benson 1983). As Molles (1980) noted, the Colorado River System may be considered "an aquatic island in a terrestrial sea". Because of long isolation, the fish fauna consists of species distinctly different from their nearest relatives, and relationships are evolutionarily and geographically distant (Miller 1959; Minckley et al. 1986). Many native genera probably existed in the basin by Miocene time, and present-day species occurred by the Plio-Pleistocene (Smith 1978; Minckley et al. 1986).

The fish fauna was first described in the middle to late 1800s in reports by naturalists assigned to military or exploratory expeditions (summarized by Evermann and Rutter 1895). Fishes native to the basin include 36 species, 20 genera, and 9 families (Table 2). Many species are polytypic within the basin.

Machete, striped mullet, and spotted sleeper are marine or brackish-water fishes that enter the Colorado's delta and ascend into the Lower Mainstem Colorado. Occurrence of spotted sleeper in the lower basin was documented by a single specimen (Hubbs 1953), and Minckley (1979) listed this species as "hypothetically" present. Ten of the remaining freshwater species are known from adjacent river basins. Of these, cutthroat trout, speckled dace, and Sonoran topminnow have subspecific representatives that are endemic to the basin. One isolated population of desert pupfish occurs naturally outside the basin (Miller 1943; Hubbs and Miller 1948; Miller 1981). The other 23 freshwater species are endemic and form an unique assemblage of highly specialized and unusual fishes. Endemic fishes account for 64 % of all native species (35 % of all native genera), constituting one of the highest levels of endemism known in North America (Miller 1959). Most other native species are represented by endemic subspecies.

Native fishes were never ubiquitously distributed throughout the basin and were associated with specific subbasins and habitat types. Many species had extremely narrow distributions within the basin (Table 2). An average of about 10 species probably occurred per major river drainage, with a range of 5 (Bill Williams drainage) to 18 or 19 (Gila River drainage). Except for mainstream species, there have always been distinct differences between upper and lower basin fish faunas. Five species (cutthroat trout, mountain whitefish, mountain sucker, mottled sculpin, and Paiute sculpin) occurred only in the upper basin and were essentially restricted to headwaters. These fishes are very similar

TABLE 2. Native fishes of the Colorado River Basin, including their current federal legal status and historic distribution/location in the basin (Evermann and Rutter 1895; Ellis 1914; Beckman 1952; Koster 1957; Miller 1959, 1961, 1972; Sigler and Miller 1963; Miller and Lowe 1964; Rinne 1976; Bailey et al. 1970; Baxter and Simon 1970; Rinne and Minckley 1970; Deacon and Bradley 1972; Minckley 1973, 1979; Holden and Stalnaker 1975; Cross 1976; Moyle 1976; Joseph et al. 1977; Behnke 1979; Deacon et al. 1979; Hubbard 1980; Lee et al. 1980; Molles 1980; Robins et al. 1980; Carothers and Minckley 1981; Parenti 1981; Behnke et al. 1982; Tyus et al. 1982; U. S. Department of the Interior 1982, 1983, 1985a-e, 1986a-e, 1987; Behnke and Benson 1983; Williams et al. 1985; Minckley et al. 1986; Stanford and Ward 1986c; Johnson 1987). X – indicates species has occurred; ? – indicates presence questionable; * – indicates endemic genera, species, or subspecies.

Species	Federal legal status^c	Historic distribution by major river drainage^a								Historic location
		Upper basin^b			Lower basin^b					
		CO	GR	SJ	CO	VR	LC	BW	GI	
ELOPIDAE										
Machete *Elops affinis*	N				X				?	sporadic in lower section of Lower Mainstem Colorado River, AZ-CA-Mexico; mouth of Gila River, AZ
SALMONIDAE										
Mountain whitefish *Prosopium williamsoni*	N		X							headwaters of Green River drainage, UT-WY-CO
Apache trout *Salmo *apache*	T						X		X	restricted to headwaters of Little Colorado and Salt rivers, AZ-NM
Colorado River cutthroat trout *S. clarki *pleuriticus*	U	X	X							headwaters of Upper Mainstem Colorado and Green river drainages, WY-CO
Gila trout *S. *gilae*	E								X	restricted to headwaters of Verde River, AZ and Gila River, NM
CYPRINIDAE										
Longfin dace *Agosia chrysogaster*	N							X	X	Bill Williams and Gila river drainages, AZ-NM, south to Rio Sonora, Mexico
Humpback chub *Gila *cypha*	E	X	X	?	X		X			larger river channels; primarily in canyon-bound segments

TABLE 2. Native fishes of the Colorado River Basin, including their current federal legal status and historic distribution/location in the basin (Evermann and Rutter 1895; Ellis 1914; Beckman 1952; Koster 1957; Miller 1959, 1961, 1972; Sigler and Miller 1963; Miller and Lowe 1964; Rinne 1976; Bailey et al. 1970; Baxter and Simon 1970; Rinne and Minckley 1970; Deacon and Bradley 1972; Minckley 1973, 1979; Holden and Stalnaker 1975; Cross 1976; Moyle 1976; Joseph et al. 1977; Behnke 1979; Deacon et al. 1979; Hubbard 1980; Lee et al. 1980; Molles 1980; Robins et al. 1980; Carothers and Minckley 1981; Parenti 1981; Behnke et al. 1982; Tyus et al. 1982; U. S. Department of the Interior 1982, 1983, 1985a-e, 1986a-e, 1987; Behnke and Benson 1983; Williams et al. 1985; Minckley et al. 1986; Stanford and Ward 1986c; Johnson 1987). X – indicates species has occurred; ? – indicates presence questionable; * – indicates endemic genera, species, or subspecies. cont'd

Species	Federal legal status[c]	Historic distribution by major river drainage[a]								Historic location
		Upper basin[b]			Lower basin[b]					
		CO	GR	SJ	CO	VR	LC	BW	GI	
Bonytail _G. *elegans_	E	X	X	X	X		X		X	larger river channels of the basin; widespread
Colorado roundtail chub _G. *robusta robusta_	N	X	X	X				X	X	medium to large-sized river channels of the basin; widespread
No common name _G. *r. grahami_[d]	U								X	status questionable; Gila River drainage
Pahranagat roundtail chub _G. *r. jordani_	E					X				restricted to springs and spring-streams of Pahranagat Valley, pluvial White River, NV
Virgin river roundtail chub _G. *r. seminuda_	P-E					X				restricted to Virgin River, AZ-NV-UT
Moapa roundtail chub _G. *r. robusta_ spp. [e]	U					X				restricted to Moapa River, NV
Gila chub _G. *intermedia_[f]	U								X	restricted to upper Gila River drainage, AZ-NM
White River spinedace _*Lepidomeda albivallis_	E					X				restricted to pluvial White River, NV
Pahranagat spinedace _*L. altivelis_	O					X				restricted to cool springs and spring-streams of Pahranagat Valley, Virgin River drainage, NV
Virgin river spinedace _*L. mollispinis mollispinis_	U					X				restricted to Virgin River drainage, AZ-NV-UT
Meadow Valley spinedace _*L. m. pratensis_	P-T					X				restricted to Meadow Valley Wash, Virgin River drainage, NV
Little Colorado spinedace _*L. vittata_	P-T						X			restricted to upper Little Colorado River drainage, AZ
Spikedace _*Meda fulgida_	T								X	moderately restricted to upper Gila River drainage, AZ-NM
Moapa dace _*Moapa coriacea_	E					X				highly restricted to thermal springs of Moapa River, NV
Woundfin _*Plagopterus argentissimus_	E				X	X			X	lower and middle sections of Lower Mainstem Colorado, Virgin, Salt, and Gila rivers

TABLE 2. Native fishes of the Colorado River Basin, including their current federal legal status and historic distribution/location in the basin (Evermann and Rutter 1895; Ellis 1914; Beckman 1952; Koster 1957; Miller 1959, 1961, 1972; Sigler and Miller 1963; Miller and Lowe 1964; Rinne 1976; Bailey et al. 1970; Baxter and Simon 1970; Rinne and Minckley 1970; Deacon and Bradley 1972; Minckley 1973, 1979; Holden and Stalnaker 1975; Cross 1976; Moyle 1976; Joseph et al. 1977; Behnke 1979; Deacon et al. 1979; Hubbard 1980; Lee et al. 1980; Molles 1980; Robins et al. 1980; Carothers and Minckley 1981; Parenti 1981; Behnke et al. 1982; Tyus et al. 1982; U. S. Department of the Interior 1982, 1983, 1985a-e, 1986a-e, 1987; Behnke and Benson 1983; Williams et al. 1985; Minckley et al. 1986; Stanford and Ward 1986c; Johnson 1987). X – indicates species has occurred; ? – indicates presence questionable; * – indicates endemic genera, species, or subspecies. cont'd

Species	Federal legal status[c]	Historic distribution by major river drainage[a]								Historic location
		Upper basin[b]			Lower basin[b]					
		CO	GR	SJ	CO	VR	LC	BW	GI	
Colorado squawfish *Ptychocheilus *lucius*	E	X	X	X	X		X		X	larger river channels of the basin; widespread
Las Vegas dace *Rhinichthyes *deaconi*	O					X				restricted to Las Vegas Valley, Virgin River drainage, NV
Southern speckled dace *R. osculus*[g] ** osculus*	N								X	southern Gila River drainage
Colorado speckled dace *R. o. *yarrowi*	N	X	X	X	X	X	X	X		middle and upper Colorado River Basin
Moapa speckled dace *R. o. *moapae*	U					X				restricted to Moapa River, NV
Pahranagat speckled dace *R. o. *velifer*	U					X				restricted to Pahranagat Valley, Virgin River drainage, NV
Kendall Warm Springs dace *R. o. *thermalis*	E		X							restricted to Kendall Warm Springs, upper Green River drainage, WY
Meadow Valley speckled dace *R. osculus**spp.	U					X				restricted to Meadow Valley Wash, Virgin River drainage, NV
Preston Spring speckled dace *R. osculus**spp.	U					X				restricted to Preston Spring, Virgin River drainage, NV
Loach minnow **Tiaroga cobitis*	P-T								X	moderately restricted to upper Gila River drainage, NV
CATOSTOMIDAE										
Sonora sucker *Catostomus *insignis*	N							X	X	moderately restricted to Bill Williams and Gila river drainages, AZ-NM
Flannelmouth sucker *C. *latipinnis*	N	X	X	X	X	X	X		X	medium to large-sized river channels of the basin; widespread
Gila mountain sucker *C. (Pantosteus*[i]*) *clarki clarki*[j]	N							X	X	Bill Williams and Gila river drainages, AZ-NM
White River sucker *c. (P.) *c. intermedius*[j]	U					X				pluvial White River, NV
Colorado bluehead sucker *c. (p.) discobolus*[k] *discobolus*	N	X	X	X	X		X			medium to large-sized river channels; widespread

TABLE 2. Native fishes of the Colorado River Basin, including their current federal legal status and historic distribution/location in the basin (Evermann and Rutter 1895; Ellis 1914; Beckman 1952; Koster 1957; Miller 1959, 1961, 1972; Sigler and Miller 1963; Miller and Lowe 1964; Rinne 1976; Bailey et al. 1970; Baxter and Simon 1970; Rinne and Minckley 1970; Deacon and Bradley 1972; Minckley 1973, 1979; Holden and Stalnaker 1975; Cross 1976; Moyle 1976; Joseph et al. 1977; Behnke 1979; Deacon et al. 1979; Hubbard 1980; Lee et al. 1980; Molles 1980; Robins et al. 1980; Carothers and Minckley 1981; Parenti 1981; Behnke et al. 1982; Tyus et al. 1982; U. S. Department of the Interior 1982, 1983, 1985a-e, 1986a-e, 1987; Behnke and Benson 1983; Williams et al. 1985; Minckley et al. 1986; Stanford and Ward 1986c; Johnson 1987). X – indicates species has occurred; ? – indicates presence questionable; * – indicates endemic genera, species, or subspecies. cont'd

Species	Federal legal status[c]	Historic distribution by major river drainage[a]								Historic location
		Upper basin[b]			Lower basin[b]					
		CO	GR	SJ	CO	VR	LC	BW	GI	
Zuni bluehead sucker _c. (P.) d._ *_yarrowi_	U						X			restricted to upper Zuni River drainage, AZ-NM
Mountain sucker _c. (P.) platyrhynchus_	N	X	X							headwaters of Upper Mainstem Colorado and Green river drainages, UT-WY-CO
Little Colorado sucker _Catostomus_ *sp.[h]	N						X			restricted to Little Colorado River drainage, AZ-NM
Razorback sucker *_Xyrauchen texanus_	U	X	X	X	X				X	larger river channels of the basin; widespread
CYPRINODONTIDAE[i]										
Northern springfish *_Crenichthys baileyi albivallis_	U					X				restricted to isolated springs and spring-streams of pluvial White river, NV
Pahranagat springfish *_C. b. baileyi_	N					X				restricted to isolated springs and spring-streams of Pahranagat Valley, pluvial White River, NV
Great springfish *_C. b. grandis_	N					X				restricted to isolated springs and spring-streams of Pahranagat Valley, pluvial White River, NV
Moapa springfish *_C. b. moapae_	U					X				restricted to isolated springs and spring-streams of pluvial White River, NV
Thermal springfish *_C. b. thermophilus_	N					X				restricted to isolated springs and spring-streams of pluvial White River, NV
Railroad Valley springfish *_C. nevadae_	T					X				Railroad Valley, a former connective of the Virgin River drainage, NV
Sonoran Desert pupfish _Cyprinodon macularius_ *_macularius_	E				X				X	lower section of Lower Mainstem Colorado River and Gila River drainage
Salton Sea pupfish _C. m._ *_californiensis_	E				X					Salton Sea Basin, CA
POECILIIDAE										
Sonoran topminnow _Poeciliopsis occidentalis occidentalis_	E								X	moderately restricted to Gila River drainage south into Mexico

TABLE 2. Native fishes of the Colorado River Basin, including their current federal legal status and historic distribution/location in the basin (Evermann and Rutter 1895; Ellis 1914; Beckman 1952; Koster 1957; Miller 1959, 1961, 1972; Sigler and Miller 1963; Miller and Lowe 1964; Rinne 1976; Bailey et al. 1970; Baxter and Simon 1970; Rinne and Minckley 1970; Deacon and Bradley 1972; Minckley 1973, 1979; Holden and Stalnaker 1975; Cross 1976; Moyle 1976; Joseph et al. 1977; Behnke 1979; Deacon et al. 1979; Hubbard 1980; Lee et al. 1980; Molles 1980; Robins et al. 1980; Carothers and Minckley 1981; Parenti 1981; Behnke et al. 1982; Tyus et al. 1982; U. S. Department of the Interior 1982, 1983, 1985a-e, 1986a-e, 1987; Behnke and Benson 1983; Williams et al. 1985; Minckley et al. 1986; Stanford and Ward 1986c; Johnson 1987). X - indicates species has occurred; ? - indicates presence questionable; * - indicates endemic genera, species, or subspecies. cont'd

Species	Federal legal status[c]	Historic distribution by major river drainage[a]								Historic location
		Upper basin[b]			Lower basin[b]					
		CO	GR	SJ	CO	VR	LC	BW	GI	
MUGILIDAE										
Striped mullet										
Mugil cephalus	N				X				X	sporadic in lower section of Lower Mainstem Colorado river, AZ-CA-Mexico; mouth of Gila River, AZ
ELEOTRIDAE										
Spotted sleeper										
Eleotris picta	N				?					extreme lower section of Lower Mainstem Colorado River, AZ-CA-Mexico
COTTIDAE										
Mottled sculpin										
*Cottus bairdi *punctulatus*	N	X	X	X						headwaters of upper basin drainages, UT-WY-CO
Paiute sculpin										
C. beldingi	N	X								headwaters of Upper Mainstem Colorado River drainage, CO
NUMBER OF SPECIES		12	12	8 (9?)	11 (12?)	12	9	5	18 (19?)	

[a] Major river drainages: CO — Mainstem Colorado, GR — Green, SJ — San Juan, VR — Virgin, LC — Little Colorado, BW — Bill Williams, GI — Gila.

[b] Dividing line at Lee Ferry, AZ.

[c] Federal legal status under the 1973 Endangered Species Act as amended: T — threatened, E — endangered, P — proposed for listing, U — under review (candidate), N — no federal status (however, certain of these taxa are variously protected by one or more basin states) O — extinct.

[d] Included here are populations referred by Rinne (1976) to *Gila robusta grahami* Girard; problematic fishes currently under study.

[e] This distinctive form may be worthy of subspecific rank, but remains under study.

[f] This taxon was raised to specific rank by Rinne (1976); an action followed by several western biologists (Rinne and Minckley 1970; Minckley 1973; Minckley et al. 1986).

[g] Many distinctive forms of speckled dace occur in the Lower Colorado River Basin, especially as "big-river" forms in most major streams and also as isolated populations in headwaters and springs. Status of these may never be determined because of complexities of their variation.

[h] The Little Colorado sucker, proposed as an undescribed species related to flannelmouth sucker by Minckley (1973), is yet to be formally described.

[i] Minckley (1973) provided reasoning for retaining *Pantosteus* as a valid genus (see Smith 1966 for the alternative view).

[j] Certain *Pantosteus* of the Bill Williams and Virgin rivers are distinctive and may represent valid species. This is especially true for the Bill Williams River, where *P. clarki* typical of the Gila River drainage co-occur with another form (Minckley 1973).

[k] As with *P. clarki*, this highly available taxon may include a number of unrecognized species.

[l] Parenti (1981) demonstrated that the United States genera *Crenichthys* and *Empetrichthys* belong to the family Goodeidae, an otherwise live-bearer family of central Mexico.

to conspecifics in adjacent river basins. Twenty species are known only from the lower basin and (excluding marine forms) were largely confined to small to medium-sized river channels. The Virgin and Gila river drainages represent centers of endemism. Only eight species were common to both the upper and lower basins. Of these, humpback chub, bonytail, Colorado squawfish, flannelmouth sucker, and razorback sucker, the so-called "big river" fishes, were generally restricted to large, mainstream channels. Biology, ecology, and habitat requirements of the basin's native fishes have been reviewed in detail by Minckley (1973, 1979), Deacon and Minckley (1974), Behnke et al. (1982), Behnke and Benson (1983), Stanford and Ward (1986c), and contributors to Spofford et al. (1980) and Miller et al. (1982a).

Merriam's vegetation zones were employed in Graf's (1985) description of natural riparian vegetation. At upper elevations in the basin, riparian communities were dominated by willows. In lower (Transition, Upper Sonoran, and Lower Sonoran) zones, riparian vegetation was a complex mix of willows (*Salix* sp.), cottonwood (*Populus* sp.), mesquite (*Prosopis* sp.), seepwillow (*Baccharis salicifolia*), and arrowweed (*Tessaria sericea*). Specific communities were described in detail by Brown et al. (1977) and Stanford and Ward (1986a). The exotic tamarisk (also known as salt cedar), *Tamarix gallica*, had been introduced to the basin and occurred in riparian communities of most drainages by 1935 (Graf 1985). A well-developed riparian community along the lower Colorado provided allochthonous organic input to the stream and furnished habitat for terrestrial insects which served as fish food. Ohmart et al. (1977) estimated that at least 2 023 ha of cottonwood communities existed along 322 km of potentially suitable habitat on the lower river in the 1600's. Overgrazing and cutting of cottonwoods and mesquite for fuel had caused significant changes in pristine riparian communities before regulation of the river (Ohmart et al. 1977). Riparian vegetation was important then, as now, in supplying habitat for terrestrial vertebrates (Johnson and Jones 1977).

Management of the Colorado River System

Native Americans began diverting water from rivers in the Colorado River Basin to irrigate crops around 1000 AD, and sophisticated canal systems existed on floodplains of the Salt, Gila, San Juan, and other streams by 1200 (Graf 1985). The early irrigators vanished by 1400, and interest in diverting water for agriculture in the Colorado basin was not renewed until the middle to late 1800s, when small diversions abounded and discussions of major diversion projects began (Fradkin 1981). Levees were constructed to contain the lower Colorado River, and jetties and frontworks were built to deflect currents and protect streamside development. Major diversions of Colorado River water to the Imperial Valley, California, began just after the turn of the century, and the Salton Sea was created when the flooding Colorado broke through restraints in 1905 (Sykes 1937; Watkins 1969).

TABLE 3. Selected decisions and projects influencing the Colorado River System (Hughes 1967; Watkins 1969; Spofford 1980; Fradkin 1981; Carlson and Carlson 1982; Harris et al. 1982; Plummer 1983; Valentine 1983; Coats 1984; Upper Colorado River Commission 1984; Graf 1985; Welsh 1985; Hundley 1986; Bureau of Reclamation data).

A. Laws, compacts, treaties and other decisions

Year	Action	Rationale/effect
1902	Reclamation (Newlands) Act passed	Created U.S. Reclamation service (Bureau of Reclamation)
1903	Salt River Project (Colorado R. to central AZ) authorized	Irrigation agriculture near Phoenix, AZ; authorized Roosevelt Dam
1904	Yuma Project (Laguna Dam) authorized	Irrigation of Yuma Valley, AZ/CA
1908	Grand Canyon National Monument established	—
1915	Dinosaur National Monument and Rocky Mountain National Park established	—
1919	Grand Canyon National Park established	—
1922	Colorado River Compact signed (AZ joined 1944)	Divided Colorado R. water between upper and lower basins[a]
1929	Boulder Canyon Project Act passed	Authorized Hoover Dam and all-American Canal; Congress approved Compact of 1922
1934	Fish and Wildlife Coordination Act passed	Provided that federal water project planning must consider impacts on wildlife
1944	Mexican Water Treaty signed	Assured Mexico of 1.85 $km^3 \cdot yr^{-1}$ of Colorado R.

B. Dams, diversions, and other structural modifications

Year	Action	Rationale/effect
1892	Grand Ditch (Colorado R. to eastern slope, CO) completed	First diversion of water from Colorado basin
1901	Imperial Canal completed (Colorado R. near Yuma, AZ, to Imperial Valley, CA)	Irrigation of Imperial Valley
1909	Laguna Diversion Dam (Colorado R., CA/AZ) completed	Irrigation of Yuma Valley, AZ/CA
1911	Roosevelt Dam and Power Plant completed (Salt R., AZ)	First high dam (multipurpose) in basin[b]
1913	Strawberry Dam (Strawberry R., UT) completed	Water storage for Provo, UT, area (Great Basin)
1915	First Imperial Irrigation District temporary diversion dam completed	Ensuring minimum flows to imperial Valley
1935	Hoover Dam completed (Colorado R., NV/AZ)	Multipurpose (water storage, flood control, and power generation)
1938	Imperial Dam (Colorado R., AZ/CA) and Parker Dam (Colorado R., CA/AZ) completed	Desilting of irrigation water to AZ and CA; water storage for southern CA and central AZ; flood control
1940	All-American Canal (Imperial Reservoir to Imperial Valley) opened	Irrigation of Imperial Valley
1941	Colorado River Aqueduct (L.	Municipal water for Los Angeles and

TABLE 3. *(Continued)*

A. Laws, compacts, treaties and other decisions		
Year	Action	Rationale/effect
		water[a]; authorized Davis Dam
1948	Upper Colorado River Basin Compact signed	Apportioned upper basin water to upper basin states and AZ[a]
1956	Colorado River Storage Project Act passed	Authorized Flaming Gorge, Glen Canyon, Navaho and Curecanti projects in upper basin
1964	*Arizona* v. *California* Supreme Court decision issued; Canyon lands National Park established	Apportioned lower basin water between AZ, CA and NV[a]
1968	Colorado River Basin Project Act passed	Authorized Central Arizona Project and five upper basin projects
1969	National Environmental Policy Act passed	Required Bureau of Reclamation to work under provisions of acts and consult with wildlife authorities
1973	Endangered Species Act passed	—
1974	Colorado River Basin Salinity Control Act passed	Controlled salinity of Colorado R. water
1982	Reclamation Act amended	Raised limitation on land owned by Bureau of Reclamation water users

B. Dams, diversions, and other structural modifications		
Year	Action	Rationale/effect
	Havasu to Southern CA)	environs
1943	Gila Project (Imperial Res. to lands along Colorado and Gila rivers) opened	Irrigation of lower Gila and Colorado Valleys
1946	Headgate Rock Diversion Dam (Colorado R., CA/AZ) completed	Irrigation of Indian lands along Colorado R.
1950	Morelos Dam (Colorado R., Mexico) completed	Storage for irrigation of Mexicali Valley, Mexico
1953	Davis Dam (Colorado R., AZ/NV) completed	Regulation of water delivery to Mexico; flood control
1963	Flaming Gorge Dam (Green R., UT) and Navaho Dam (San Juan R., CO) completed	Multipurpose
1964	Glen Canyon Dam (Colorado R., AZ) and Fontenelle Dam (Green R., WY) completed	Multipurpose
1977	Bypass drain (Colorado R. to Gulf of California) opened	Diverting brackish water from Colorado R.
1978	Crystal Reservoir (Gunnison R., CO); Curecanti Unit (name changed to Wayne Aspinall Storage Unit 1980) completed	Storage
—	Under construction Yuma Desalting Plant; central Arizona Project (L. Havasu to Pheonix)	Desalting water; supplying water to central AZ and to central NV and UT.

[a] See Graf (1985) for legal water entitlements to basins, states and Mexico.

[b] See Graf (1985) for heights and storage capacities of major high dams in the Colorado system.

The U.S. Bureau of Reclamation, created by legislative action in 1902 (Table 3A), is responsible for construction and operation of projects that support economic development, primarily irrigation agriculture and industrial water uses (Graf 1985). Fradkin (1981) referred to five phases of the Bureau's "conquest" of the Colorado River. First, it constructed several small, non-controversial projects and followed these with the larger Strawberry Valley Project, Utah; Gunnison Tunnel, Colorado; Roosevelt Dam, Arizona; and Laguna Dam on the lower Colorado (Table 3B). Plans to enhance irrigation of the Imperial Valley by building a new canal (within the borders of the United States) and large reservoirs on the river to store water, control floods, and produce power led to fears in upper-basin states that the lower basin would claim rights to all water in the river under the doctrine of prior appropriation. Discussions culminated in the Colorado River Compact, which divided waters between the upper and lower basins (above and below Lee Ferry, respectively) on the basis of estimated virgin flows at Lee Ferry from 1896 to 1921. Negotiators based allocations on an annual flow of at least 22.20 km^3 (Hundley 1966). Average annual virgin flow at Lee Ferry is now estimated at 20.72 km^3 for the pre-Compact period and 17.52 km^3 since 1922 (Upper Colorado River Commission 1984). The Colorado's waters were overcommitted by this first attempt at apportionment.

After a period of stagnation through the 1920's, the Bureau of Reclamation launched its major dam-building era (the second phase of its conquest of the river) with passage of the Boulder Canyon Project Act in 1929 (Fradkin 1981). That law and the Upper Colorado River Basin Compact apportioned waters among states in the lower and upper basins, respectively, and Mexico was guaranteed water from the Colorado River by the Mexican Water Treaty (Graf 1985). High dams in the upper basin were authorized by the Colorado River Storage Project Act of 1956. Plans to construct dams at Echo Park in Dinosaur National Monument and at Bridge and Marble canyons in Grand Canyon were scuttled when public opinion stimulated by Wilderness Society and Sierra Club advertising reached U.S. congressmen (Watkins 1969; Nash 1970; Coats 1984). Welsh (1985) described the prolonged controversy over the Central Arizona Project and withdrawal of funding for Orme Dam.

The Bureau entered its third phase of conquest, construction of large aqueducts to deliver water to local areas, with passage of the Colorado River Basin Project Act of 1968. Fradkin's (1981) fourth phase, designed to "clean up the mess" caused by preceding phases, was launched by passage of the Colorado River Basin Salinity Control Act in 1974. The final phase will involve increasing the amount of water in the Colorado River Basin by imports from other basins or augmenting runoff through weather modification, strategies which will require additional study and negotiation (Pillsbury 1981; Harris 1983).

Since closure of Hoover Dam, the Colorado River System has become one of the most intensively controlled in the United States (Petts 1984). Although high dams provide security and profit for humans in the southwestern United States (Graf 1985), they have also transformed most of the streams in the Colorado basin into man-made rivers (Petts 1984).

Modifications documented in Table 3 B represent only the "tip of the iceberg" of man-induced changes in the Colorado River System. Bishop and Porcella (1980) reported some 117 reservoirs with individual storage capacities over 0.001 km^3 in the upper basin alone and about 40 trans-mountain canals and tunnels exporting water from that region. Water from the Colorado River Basin has long been diverted to and used in the Arkansas, Platte, and Rio Grande river basins and the Great Basin. On the lower Colorado, channels have been shortened by excavation, banks rip-rapped, and channels deepened by dredging (Minckley 1979). Lowering of water tables due to groundwater pumping, diversion and modification of spring runs, channelization, and impoundments have reduced fish habitats in desert portions of the Colorado basin (Pister 1981; Meffe et al. 1983; Williams et al. 1985).

Reservoir construction and diversion of water (often in open canals) from streams in the Colorado River Basin have enormously increased evaporative water loss from the system (Welsh 1985). Twelve percent of the Colorado's annual flow evaporated from reservoirs by the 1970's, and another 3% was diverted from the basin (Graf 1985). Weatherford and Brown (1986) noted that 6.16 km^3 of water are exported from the basin annually. These phenomena team with crop irrigation and effects of municipal and industrial water uses to exacerbate natural downstream salinity increases (Carlson and Carlson 1982). High salinity, the river's most serious water quality problem, increases costs of water use and adversely affects agricultural productivity (Graf 1985).

By 1974, salt concentrations in the lower river had reached maximum levels recommended for agriculture and human consumption, and basin states agreed upon a program to maintain salinity at or below levels measured near lower-basin mainstream dams in 1972. The Colorado River Basin Salinity Control Act restricted salinity of water delivered to Mexico at Morelos Dam (Pillsbury 1981). A canal was constructed to divert highly saline water from the Welton-Mohawk Irrigation District to the Gulf of California, and the Bureau of Reclamation is building a desalting plant at Yuma, Arizona, to ensure delivery of required flows and salinities to Mexico. Such projects are expected to reduce TDS by 130 mg$\cdot$L^{-1} at Imperial Dam (Paulson and Baker 1983).

Increased use of Colorado River water has also caused local problems associated with high heavy metals concentrations, radioactive materials, acid mine drainage, and oxygen levels near waste-treatment facilities (Bishop and Porcella 1980; Graf 1985). Additional energy development in the upper basin will increase impacts related to mining and rapid urbanization (Spofford et al. 1980; Jacobsen 1982; Adams and Lamarra 1983), and acid deposition may become a serious problem.

Watkins (1969) and Carothers and Johnson (1983) recognized the conflict between increasing visitation to National Park System areas in the Colorado River Basin and preservation of natural qualities of such lands. The National Park Service, Forest Service, and Bureau of Land Management now impose quotas on river rafters (Coats 1984) and enforce strict regulations on camping areas, use of fires, and waste management on lands they administer (Graf 1985). Nash (1986) emphasized the need to protect the Colorado's remaining wilderness.

The Colorado River Today

The Colorado River Basin is largely an area of very low human population density. It has few large cities but is highly urbanized; only 20% of its population is rural (Graf 1985). Most of the land in the basin is administered by the United States government, primarily as Indian reservations, National Park System lands, national forests, and Bureau of Land Management (BLM) areas. The basin includes nine national parks, four recreation areas, 25 national monuments, and huge tracts of national forest and BLM-administered grazing or mineral-bearing lands (Graf 1985).

The present-day Colorado River supplies more water for consumptive use than any other river in the United States (Pillsbury 1981) despite having the lowest unit-area discharge (28 575 m$^3\cdot$km^{-2}) of any United States river basin (Bishop and Porcella 1980). Stanford and Ward (1986a) referred to the basin as one of the driest in the world.

The long-term (1896-1984) estimated annual average virgin flow of the Colorado River at Lee Ferry was 18.26 km^3, but 1983 and 1984 levels were 29.60 and 30.22 km^3, respectively (Upper Colorado River Commission 1984). Stream regulation in the basin has reduced high spring flows and resulted in relatively high summer flows; drastic daily variation is common (Graf 1985). The Colorado River below Glen Canyon Dam may rise as much as 1.8 m in a few minutes, but potential for ecological damage in the Grand Canyon has no bearing on the dam's operating criteria (Coats 1984). Less than one percent of the river's virgin flow now reaches its mouth (Petts 1984).

Dams have also changed the capacity of streams in the Colorado River System to transport sediments. Sediments previously moved by streams are deposited in reservoirs, and space intended for water storage is gradually reduced as they accumulate (Graf 1985). Flows released from dams are relatively clear as well as seasonally constant; an excellent example is provided by data collected before and after closure of Glen Canyon Dam (Table 4).

Studies at several mainstream Colorado River dams (Petts 1984) have demonstrated that rapid degradation of channels may extend for many kilometres downstream from dams releasing frequent and prolonged outflows of clear water. Regulated flows have, thereby, changed channel forms and armoured stream bottoms in tailwaters (Graf 1985; Stanford and Ward 1986a). Numbers and sizes of mid-channel bars or islands and channelside bars or beaches have also been reduced below dams (Graf 1985). By limiting ability of streams to move coarse material, flow regulation has led to stabilized rapids downstream from dams (Graf 1985; Stanford and Ward 1983) and accumulation of sediments discharged from tributaries to mainstream channels (Dolan et al. 1974; Howard and Dolan 1981). Reductions in peak flow and channel and bank modifications have reduced the extent of backwaters and marshes.

Regulation has lowered mainstream water temperatures 10–15°C and resulted in cooler summer and warmer winter water temperatures below dams (Stanford and Ward 1986a). Lowered summer temperatures have adversely affected native fishes below Flaming Gorge and Glen Canyon dams (Kaeding and Zimmerman 1983).

By 1957, natural salt levels (about 250 mg•L^{-1}) at Lee Ferry had doubled (Graf 1985). Welsh (1985) reported a salt concentration of 600 mg•L^{-1} below Lake Powell and noted that the Central Arizona Project will extract water with 750 mg•L^{-1} from below Lake Mead. Paulson and Baker (1983) reported salinity of 825 mg•L^{-1} at Imperial Dam. Sulfate constitutes nearly half of the TDS in the Colorado River but has little effect on agriculture or municipal water uses.

Paulson (1983) discussed means of reducing TDS in and evaporation from Lake Mead by regulating releases from Lake Powell at Glen Canyon Dam. Lake Powell construction and regulation have affected a marked reduction in phosphorus transport to and productivity in Lake Mead 450 km downstream (Evans and Paulson 1983; Prentki and Paulson 1983; Stanford and Ward 1986b). A decline in the fishery of Lake Mead has been partly attributed to the reservoir's diminished fertility (Baker and Paulson 1983). Production in Colorado River reservoirs is strongly influenced by physicochemistry of river inflows (Stanford and Ward 1986b).

More uniform water temperatures and reduction in backwater and marsh habitat can be expected to diminish the frequency and severity of oxygen depletions in the Colorado River System. However, river regulation has introduced potential for downstream release from reservoirs of waters supersaturated with air gases; these could have detrimental effects on aquatic life (Holden 1979).

Aquatic flora and invertebrate fauna of few mainstream reaches of the Colorado River have been studied. Ward et al. (1986) stated that the filamentous green alga, *Cladophora glomerata*, is common on solid surfaces for several kilometers below dams in the basin. The cooler and less turbid waters in the Grand Canyon are now characterized by dense bottom mats of this alga, which is little used by most invertebrates but provides food for introduced fishes (Carothers and Minckley 1981; Carothers and Dolan 1982). The alga provides habitat and food for diatoms and the non-native *Gammarus lacustris*, a common mainstream invertebrate. Benthic invertebrate productivity and diversity in the Grand Canyon are low, and the main river lacks many common invertebrate groups found in tributaries.

Ward et al. (1986) reviewed studies of lotic zoobenthos in the mainstem Colorado River and at 34 tributary loca-

TABLE 4. Hydrological and sediment transport characteristics of the Colorado River below Glen Canyon Dam (modified from Dolan et al. 1974 and Petts 1984).

	Lee Ferry (24 km downstream)		Grand Canyon (165 km downstream)	
	Pre-dam	Post-dam	Pre-dam	Post-dam
Daily average flow equalled or exceeded 95 % of the time (m^3•s^{-1})	102	156	113	167
Median discharge (m^3•s^{-1})	209	345	232	362
Mean annual flood (m^3•s^{-1})	2 434	764	2 434	792
10 year's flood (m^3•s^{-1})	3 481	849	3 453	1 132
Annual maximum stage (m):				
Mean	5.04	3.56	6.89	4.79
Standard deviation	0.96	0.17	0.35	0.15
Annual minimum stage (m):				
Mean	1.76	1.46	0.46	0.70
Standard deviation	1.40	0.23	0.85	0.45
Mean sediment concentration (mg•L^{-1})	1 500	7	1 250	350
Sediment concentration equalled or exceeded 1 % of the time (mg•L^{-1})	21 000	700	28 000	15 000

tions. Chironomids, baetid mayflies, amphipods, planarians, oligochaetes, and snails tend to be predominant in tailwaters below deep-release dams. Common benthic invertebrates in potamon reaches in the upper basin and lower river are oligochaetes, chironomids, gastropods, leeches, turbellarians, sphaeriid clams, odonates, beetles, simuliids, net-spinning caddisflies, and baetid mayflies. Introduced freshwater shrimp and crayfishes are locally abundant in the lower river, and the introduced Asiatic clam, *Corbicula fluminea*, occurs as far upstream as Lake Mead. The Colorado River System appears unique in that unionacean clams are virtually absent from its waters and isopods are usually absent from lotic sites.

The fish fauna of the Colorado River Basin bears little resemblance to its original state. Approximately 100 species are now present; some 67 non-native fish species in 16 families have been introduced since the turn of the century and are now predominant in most fish communities (Miller and Lowe 1964; Minckley 1973, 1979; Moyle 1976; Carothers and Minckley 1981; Tyus et al. 1982). In terms of numbers of species, cyprinids, centrarchids, salmonids, catostomids, and ictalurids head the list of introduced fishes. Of the 54 natives listed in Table 2, 17 are either threatened, endangered, or extinct, and most have experienced drastic abundance and range reductions (Miller 1972; Minckley 1973, 1979; Joseph et al. 1977; Behnke and Benson 1983). Two species (Pahranagat spinedace and Las Vegas dace) are extinct, and the woundfin is almost gone. The cutthroat trout is threatened in the upper basin (Behnke 1979), and most stream- and spring-inhabiting fishes of the middle and lowermost Colorado River drainage are legally protected or of special concern (Johnson 1987). All of the "big-river" fishes are in jeopardy (Minckley 1973, 1983; Carothers and Minckley 1981; Tyus et al. 1982; Behnke and Benson 1983; Hickman 1983). Wild Colorado squawfish are gone from the lower basin, and the flannelmouth sucker is extirpated from the Gila River drainage (Williams et al. 1985). Tyus (1987) considered razorback sucker one of the rarest fishes in the Colorado River Basin. The humpback chub persists tenuously in the Little Colorado River and Grand Canyon (Kaeding and Zimmerman 1983) and occupies a few scattered canyon areas in the upper basin (Behnke and Benson 1983). The bonytail, originally widespread and abundant in the basin, is functionally extinct; a few scattered individuals exist in the Green and Upper Mainstem Colorado rivers and in Lake Mohave in the lower basin (Behnke and Benson 1983). Behnke and Benson (1983), said of the bonytail's demise that "If it were not for the stark example provided by the passenger pigeon, such rapid disappearance of a species once so abundant would be almost beyond belief". Several authors (Minckley 1979; Behnke 1980; Hubbard 1980; Molles 1980; Behnke and Benson 1983; Williams et al. 1985; Stanford and Ward 1986c) have attributed decline of native fishes to (1) modification and loss of habitat and (2) introduction of non-native species.

Construction and regulation of dams have had severe impacts on the fish fauna of the Colorado River, and little unaltered habitat remains (Tyus 1984). Coats (1984) described general lack of regard for minimum flow needs of fishes in operating Colorado River dams. Extreme fluctuations and alteration of seasonal flow regimes have been implicated in alleged loss of 1983 and 1984 year classes of the Colorado squawfish in its most productive remaining nursery habitat (Jones and Tyus 1985).

Williams et al. (1985) discussed adverse impacts of introduction of non-native species on native fishes in most of the 15 aquatic ecosystems in North American deserts that they considered. Schoenherr (1981) described behavioral interactions between introduced redbelly tilapia, *Tilapia zillii*, and sailfin molly, *Poecilia latipinna*, leading to replacement of desert pupfish. Schoenherr (1981), Minckley et al. (1977); Meffe et al. (1983), and Meffe (1984, 1985) studied predation by mosquitofish, *Gambusia affinis*, resulting in endangerment of Sonoran topminnow. Behnke and Benson (1983) discussed possible redside shiner, *Richardsonius balteatus*, competition with Colorado squawfish in the upper basin. Colorado squawfish interactions with other non-natives, e.g., "choking" on channel catfish, *Ictalurus punctatus*, (McAda 1983; Pimentel et al. 1985) and competition with northern pike, *Esox lucius*, (Wick et al. 1985) need further research.

Surveys by Moffett (1942, 1943), Dill (1944), and Wallis (1951), stimulated stocking of game fishes, and threadfin shad (*Dorosoma petenense*), and various invertebrates were stocked as forage. Trouts (*Salmo gairdneri, S. clarki,* and *Salvelinus fontinalis*) and Pacific salmon (*Oncorhynchus kisutch* and *O. nerka*) were stocked in reservoirs, and coldwater fisheries developed. Striped bass, *Morone saxatilis*, were introduced in Lake Mead in 1969, and a successful fishery developed in the 1970's. Rainbow trout and threadfin shad populations declined as a result of predation by striped bass (Baker and Paulson 1983).

A number of attempts were made to remove "coarse" fishes to make room for introduced species. In 1962, 700–800 km of the Green River and its tributaries were treated with rotenone to allow Flaming Gorge Reservoir and the streams to realize their full potentials as trout fisheries (Miller 1963; Dexter 1965; Pearson et al. 1968). Downstream detoxification failed, and rare endemic fishes were killed in Dinosaur National Monument. Binns (1967) reported that Colorado squawfish, razorback sucker, and rare mayflies had not reestablished populations in the treated area after 2 yr. Rotenone was also applied in the San Juan River prior to closure of Navaho Reservoir and on the Gila River upstream from San Carlos Reservoir. Impacts of these incidents have never been fully assessed.

Non-native trout fisheries downstream from Colorado River dams (Mullan et al. 1976) have become valuable assets. Flaming Gorge Dam has been modified to improve such a fishery through increase in tailwater temperatures (Holden 1979).

Other fisheries in the Colorado River Basin are dependent on non-native centrarchids and striped bass, but fishing for channel and flathead catfish (*Pylodictis olivaris*), walleye (*Stizostedion vitreum*), and northern pike is popular locally (Behnke et al. 1982; Stanford and Ward 1986c). Threadfin shad are important as food for piscivores in Lake Powell and lower-basin reservoirs (Johnson 1970, 1971; Stanford and Ward 1986c). Martin et al. (1982) estimated the annual economic value of Lake Mead fisheries at $69 million. Mullan et al. (1976), Carothers and Dolan (1982), Persons and Bulkley (1982), Morgenson (1983), and Baker and Paulson (1983) considered fishery management and cited similar studies on the Colorado system.

Studies of fish production in the system are rare. Scarnecchia and Bergersen (1986) estimated production (2.2 and 3.6 $g \cdot m^{-2}$ in 1979 and 1980, respectively) of Colorado River cutthroat trout in a headwater tributary of the Colorado River and concluded that biomass and production were dependent on stream-specific physical properties.

The Endangered Species Act of 1973 mandated efforts to maintain rare native fishes and their habitats in the Colorado basin. Listing of fishes stimulated studies of their basic biology. Information on distribution and relative abundance of fishes in the Upper Colorado River System was compiled by Tyus et al. (1982). Behnke et al. (1982) provided supplemental information on fishes of the Green and Upper Mainstem Colorado sub-basins.

Recent reports on fishes of the Colorado River System have concentrated on reproduction (Morgensen 1983; McAda and Wydoski 1983, 1985; Nesler et al. 1988), early life history (Haynes et al. 1984), marking (Muth et al. 1988), life-history strategies (Constantz 1979, 1981), foods and feeding (Barber and Minckley 1983; Marsh 1987), artificial propagation (Hamman 1985a, 1985b, 1986; Berry 1984; Muth et al. 1985), and conserving genetic diversity (Vrijenhoek et al. 1985). Culture efforts have focused on preservation of genetic material of rare fishes, description of early life stages (sensu Snyder 1981), or reintroduction of extirpated fishes within their native ranges (Minckley 1983; Johnson 1985). Migrations of Colorado squawfish to restricted upper-basin spawning grounds have been documented (Tyus and McAda 1984; Tyus 1985; Haynes and Bennett 1986). Other reports relate to responses of native fishes to temperature changes (Bulkley and Pimentel 1983; Ihnat and Bulkley 1984; Black and Bulkley 1985a, 1985b; Marsh 1985) and toxic retorted oil shale (Woodward et al. 1985) associated with dams and energy development, respectively. Amin (1968), Marsh and Rinne (1983), and Haynes and Muth (1985) noted fish spinal deformities which may be associated with altered ecosystems. Much information on upper-basin fishes has resulted from field studies through the Colorado River Fisheries Project (Miller et al. 1982b-d), while emphasis in the lower basin has been on acquisition of habitats and brood stocks, production, and reintroduction (Johnson and Rinne 1982; Johnson 1985).

Recovery of native Colorado River fishes is the responsibility of the U. S. Fish and Wildlife Service. The Recovery Implementation Task Group of the Upper Colorado River Basin Coordinating Committee and an ad hoc recovery team for lower basin fishes spearhead recovery efforts. A Desert Fishes Recovery Team deals with native species of North American deserts within the basin.

Since 1935, riparian vegetation along Colorado basin streams has been modified by water management, grazing of cattle, competitive interactions involving tamarisk, and phreatophyte removal to conserve groundwater (Ohmart et al. 1977; Brown et al. 1977; Graf 1985; Stanford and Ward 1986a). Tamarisk has competed effectively with native riparian plants since its appearance on the Salt River near Phoenix in the 1890s. It has spread northward at an average rate of 20 $km \cdot yr^{-1}$ (Graf 1985) and is becoming established on beaches along the lower Yampa River (Haynes and Bennett (1986). It has had greatest impact in the central and lower portions of the basin, where it occurs in dense thickets which have replaced willows and cottonwoods on sandbars and banks. Stream regulation has favored tamarisk expansion along fluctuating reservoir shorelines. Ill-advised efforts to salvage water through phreatophyte control have occurred in the Colorado River Basin, and millions of dollars have been spent on such clearing projects in the southwestern United States over the past 40 yr (Graf 1985).

Ohmart et al. (1977) observed that cottonwood communities along the lower Colorado River have been reduced to a precarious state. Only about 1 130 ha of cottonwood-willow communities remain, and less than 202 ha can be considered pure cottonwood communities.

Regulated outflows from high dams may create more favorable environments for riparian vegetation (Turner and Karpiscak 1980). Below Glen Canyon Dam, woody plants unable to withstand yearly inundation or grow on unstable substrates are colonizing previously inhospitable river banks (Carothers and Johnson 1983). New strips of woody vegetation extending from Glen Canyon Dam to Lake Mead grow on sediments of unknown stability deposited before construction of Glen Canyon Dam; the wildlife they support are an unexpected benefit from regulation (Carothers and Johnson 1983). A post-dam ecological equilibrium has not been achieved along the Colorado River in Grand Canyon, and establishment of a stable riparian community may require decades (Turner and Karpiscak 1980).

Recommendations for the Future

The future for the Colorado River is certain to be replete with conflicts. Coats (1984) observed that basin water is overappropriated, and there are no immediate prospects of importations from other basins. Therefore, new consumptive water uses must take water from existing ones. Conflicts will intensify between wilderness values and instream water uses, agriculture and other uses, and economic efficiency and social equity. Future shocks to the system, such as prolonged drought, energy crisis, establishment of native American water entitlements, or large-scale sales of water across state boundaries could exacerbate conflicts (White 1986). Potential solutions include importation of new water supplies (study is prohibited until 1988 by Central Arizona Project legislation), market pricing of water, managing groundwater and surface water as a single system, implementing water conservation technologies, and renegotiating the Colorado River Compact to remedy mistakes concerning river discharge and disincentives for conservation in the upper basin (Coats 1984; White 1986). Parts of the Colorado River System might be added to the Wild and Scenic River System and responsibilities of the Bureau of Reclamation broadened to include such social goals as water conservation and instream use protection.

We consider conflicts between development and natural ecosystems paramount and find it difficult to be optimistic about the remaining natural elements of the Colorado River. All agencies working toward recovery of rare native fishes of the Colorado River System have established goals and priorities for research and management. There is need for further biological research (emphasizing threatened and endangered fishes) on population dynamics, homing mechanisms, interactions involving native and non-native species, habitat requirements of all life-history stages, responses to potential water-quality modifications, and potential value of management strategies. Monitoring schemes to routinely assess the status of threatened and endangered fishes should be developed for use by basin-wide recovery teams. Research and management in the river system as a whole should be reviewed and coordinated by a single panel, and peer review and publication of results in refereed journals must receive greater emphasis.

Beyond the need for research is that for rehabilitation (sensu Regier et al. 1989). A water budget for the system and consideration of requirements of aquatic organisms in water management are needed. Remediation to benefit big-river fishes of the upper basin should include habitat manipulations and fish passage facilities (Valdez and Wick 1983; Tyus 1984; Tyus et al. 1984; Berry and Pimentel 1985; US Department of the Interior 1986a). The importance of instream flow needs of rare fishes has been recognized, and flow release from Flaming Gorge Dam was managed to improve spawning and survival of endangered fishes in 1986. Introduction of non-native fishes should be curtailed, and stocking of hatchery-reared natives considered only after careful research (Tyus 1984). In the lower basin, preservation of free-flowing riverine areas and protected refugia and management of non-native species are needed to maintain viable populations of native fishes (Williams et al. 1985). Reintroductions of rare native species and attempts to remove non-natives (Meffe 1983) should be handled in a responsible manner. Meffe's (1986) suggestions for genetically sound management of endangered fishes also deserve consideration.

Public education programs on the condition of the river and its unique, jeopardized biota are also needed. Greater cooperation between all political entities and agencies responsible for management of the system will be required if elements of that unique biota are to be preserved.

Conclusion

Research on the biota of the Colorado River System has been largely descriptive. Little is known regarding productivity, yield, and economics of the system's fisheries. Despite calls for consideration and testing of ecological concepts (Carlson et al. 1979; Ward and Stanford 1983), only a few examples of such research exist for the system (Molles 1980; Annear and Neuhold 1983). Ward et al. (1986) concluded that the Colorado system generally lacked the structural and functional integrity of eastern woodland streams on which the river continuum concept is based. Continued research should be supplemented by rehabilitation of the system.

The Colorado River has been drastically altered in less than a century of human activity, and ecological relationships have been changed most significantly in the past 50 yr. Stanford and Ward (1986a) stated that the future of this regulated system depends on whether (1) there will be enough water to maintain desirable ecosystem values and (2) native and non-native fishes can co-exist. Welsh (1985) was convinced that a future water shortage will occur in the basin and that the upper basin states, which have not yet developed their allocations, will play a major role in determining its timing. The basin is expected to experience a surface-water shortage sometime after the year 2000 unless its water supplies can be augmented. Stanford and Ward (1986a) concluded that endangered endemic fishes are incompatible with stream regulation and non-native species and that future water shortages will preclude allocations for them and other ecological concerns. Alternative scenarios might include legal provisions to protect or restore affected aquatic communities as a result of increased citizen awareness of and concern for natural values and species survival. Limits on humans population growth and development in the Southwest may also be imposed by water supply and/or other factors before the biota of the Colorado River system is significantly changed from its current status.

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References

ADAMS, V. D., AND V. A. LAMARRA [ed.] 1983. Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI. 697 p.

AMIN, O. M. 1968. Deformed individuals of two species of suckers, *Catostomus insignis* and *C. clarkii*, from the Gila River System, Arizona. Copeia 1968: 862–863.

ANNEAR, T. C., AND J. M. NEUHOLD. 1983. Characterization of Yampa and Green River ecosystem: a systems approach to aquatic resource management, p. 181–192. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI.

BAILEY, R. M., J. E. FITCH, E. S. HERALD, E. A. LACHER, C. C. LINDSEY, C. R. ROBINS, AND W. B. SCOTT. 1970. A list of common and scientific names of fishes from the United States and Canada. Am. Fish. Soc. Spec. Publ. 6: 150 p.

BAKER, J. R., AND L. J. PAULSON. 1983. The effects of limited food availability on the striped bass fishery in Lake Mead, p. 551–561. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI.

BARBER, W. E., AND W. L. MINCKLEY. 1983. Feeding ecology of a southwestern cyprinid fish, the spikedace, *Meda fulgida* Girard. Southwest. Nat. 28: 33–40.

BAXTER, G. T., AND J. R. SIMON. 1970. Wyoming fishes. Bull. 4, Wyoming Game and Fish Dep., Cheyenne, WY. 168 p.

BECKMAN, W. C. 1952. Guide to the fishes of Colorado. Univ. Colo. Mus. Leaf. 11: 110 p.

BEHNKE, R. J. 1979. Monograph of the native trouts of the genus *Salmo* of western North America. U.S. Forest Service, Lakewood, CO. 163 p. (Available from Regional Forester, 11177 West 8th Avenue, P. O. Box 25127, Lakewood, CO 80225)

1980. The impacts of habitat alterations on the endangered and threatened fishes of the Upper Colorado River Basin, p. 204–216. *In* W. O. Spofford, A. L. Parker, and A. V. Kneese [ed.] Energy development in the Southwest — problems of water, fish and wildlife in the Upper Colorado River Basin, vol. 2. Resources for the Future, Washington, DC.

BEHNKE, R. J., C. A. CARLSON, D. L. MILLER, D. E. SNYDER, E. J. WICK, AND L. D. ZUCKERMAN. 1982. A survey and analysis of existing information on fishes in Northwest Colorado, Vol. 6. *In* D. W. Crumpacker [ed.] Wildlife conservation and energy development in northwest Colorado. Ecological Services Section, Colorado Division of Wildlife, Denver, CO. (Available from Colorado Division of Wildlife, 6060 Broadway, Denver, CO 80216)

Behnke, R. J., and D. E. Benson. 1983. Endangered and threatened fishes of the Upper Colorado River Basin. Colo. State Univ. Coop. Ext. Serv. Bull. 503A: 38 p.

Berry, C. R. 1984. Hematology of four rare Colorado River fishes. Copeia 1984: 790–793.

Berry, C. R. and R. Pimentel. 1985. Swimming performances of three rare Colorado River fishes. Trans. Am. Fish. Soc. 114: 397–402.

Binns, N. A. 1967. Effects of rotenone treatment on the fauna of the Green River, Wyoming. Wyo. Game Fish Dep. Fish. Res. Bull. 1: 114 p.

Bishop, A. B., and D. P. Porcella. 1980. Physical and ecological aspects of the Upper Colorado River Basin, p. 17–56. *In* W. O. Spofford, A. L. Parker, and A. V. Kneese [ed.] Energy development in the Southwest — problems of water, fish and wildlife in the Upper Colorado River Basin, vol. 1. Resources for the Future, Washington, DC.

Black, T., and R. V. Bulkley. 1985a. Growth rate of yearling Colorado squawfish at different water temperatures. Southwest. Nat. 30: 253–257.

1985b. Preferred temperature of yearling Colorado squawfish. Southwest. Nat. 30: 95–100.

Bolton, H. E. [ed. and annotator] 1919. Kino's historical memoir of Pimeria Alta. 2 vols. Arthur H. Clark Co., Cleveland, OH. 379; 329 p.

Brown, D. E., C. H. Lowe, and J. F. Hausler. 1977. Southwestern riparian communities: their biotic importance and management in Arizona, p. 201–211. *In* Johnson, R. R. and D. A. Jones [tech. coord.] Importance, preservation and management of riparian habitats: a symposium. Gen. Tech. Rep. RM-43, Rocky Mt. For. Range Exp. Sta., Ft. Collins, CO.

Bulkley, R. V., and R. Pimentel. 1983. Temperature preferences and avoidance by adult razorback suckers. Trans. Am. Fish. Soc. 112: 601–607.

Carlson, C. A., C. G. Prewitt, D. E. Snyder, E. J. Wick, E. L. Ames, and W. D. Fronk. 1979. Fishes and macroinvertebrates of the White and Yampa rivers, Colorado. Colo. Office, US Bur. Land Manage. Biol. Sci. Ser. 1: 276 p.

Carlson, C. A., and E. M. Carlson. 1982. Review of selected literature on the Upper Colorado River System and its fishes, p. 1–8. *In* W. H. Miller, H. M. Tyus, and C. A. Carlson [ed.] Fishes of the Upper Colorado River System: present and future. Western Division, American Fisheries Society, Bethesda, MD.

Carothers, S. W., and C. O. Minckley. 1981. A survey of the aquatic flora and fauna of the Grand Canyon. Water and Power Resources Service, Boulder City, NV. 401 p. (Available from US Bureau of Reclamation, Lower Colorado River Region, P.O. Box 427, Boulder City, NV 89005)

Carothers, S. W., and R. Dolan. 1982. Dam changes on the Colorado River. Nat. History 91: 74–83.

Carothers, S. W., and R. R. Johnson. 1983. Status of the Colorado River ecosystem in Grand Canyon National Park and Glen Canyon National Recreation Area, p. 139–160. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI.

Coats, R. 1984. The Colorado River — river of controversy. Environ. 26: 6–13, 36–40.

Constantz, G. D. 1979. Life history patterns of a liverbearing fish in contrasting environments. Oecologia 40: 189–201.

1981. Life history patterns of desert fishes, p. 237–281. *In* R. J. Naiman and D. L. Soltz [ed.] Fishes in North American deserts. J. Wiley & Sons, New York, NY.

Cross, J. 1976. Status of native fish fauna of the Moapa River (Clark County, Nevada). Trans. Am. Fish. Soc. 105: 505–508.

Deacon, J., and W. Bradley. 1972. Ecological distribution of fishes of Moapa (Muddy) River in Clark County, Nevada. Trans. Am. Fish. Soc. 101: 408–419.

Deacon, J. E., and W. L. Minckley 1974. Desert fishes, p. 385–488. *In* G. W. Brown [ed.] Desert biology, vol. 2. Academic Press, New York, NY.

Deacon, J. E., G. Kobetich, J. D. Williams, S. Contreras, and others. 1979. Fishes of North America endangered, threatened, or of special concern: 1979. Fisheries 4 (2): 29–44.

Dexter, W. D. 1965. Some effects of rotenone treatment on the fauna of the Green River, Wyoming. Proc. Annu. Conf. West. Assoc. State Game Fish Comm. 45: 193–197.

Dill, W. A. 1944. The fishery of the lower Colorado River. Calif. Fish Game 30: 109–211.

Dolan, R., A. Howard, and A. Gallenson. 1974. Man's impact on the Colorado River in the Grand Canyon. Am. Sci. 62: 392–401.

Ellis, M. M. 1914. Fishes of Colorado. Univ. Colo. Stud. 11: 136 p.

Evans, T. D., and L. J. Paulson. 1983. The influence of Lake Powell on the suspended sediment-phosphorus dynamics of the Colorado River inflow to Lake Mead, p. 57–68. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI.

Evermann, B. W., and C. Rutter. 1895. Fishes of the Colorado Basin. US Fish Comm. Bull. 14: 473–486.

Fradkin, P. L. 1981. A river no more — the Colorado River and the West. Knopf, New York, NY. 360 p.

Graf, W. L. 1985. The Colorado River — instability and basin management. Association of American Geographers, Washington, DC. 86 p.

Hamman, R. L. 1985a. Induced spawning of hatchery-reared razorback sucker. Progr. Fish-Cult. 47: 187–189.

1985b. Induced spawning of hatchery-reared bonytail. Progr. Fish-Cult. 47: 239–241.

1986. Induced spawning of hatchery-reared Colorado squawfish. Progr. Fish-Cult. 48: 72–74.

Harris. E. R. 1983. Environmental and social implications of cloud seeding in the Colorado River Basin, p. 249–258. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI.

Harris, R. E., H. N. Sersland, and F. P. Sharpe. 1982. Providing water for endangered fishes in the Upper Colorado River System, p. 90–92. *In* W. H. Miller, H. M. Tyus, and C. A. Carlson [ed.] Fishes of the Upper Colorado River System: present and future. Western Division, American Fisheries Society, Bethesda, MD.

Haynes, C. M., T. A. Lytle, E. J. Wick, and R. T. Muth. 1984. Larval Colorado squawfish (*Ptychocheilus lucius* Girard) in the Upper Colorado River Basin, Colorado, 1979–1981. Southwest. Nat. 29: 21–33.

Haynes, C. M., and R. T. Muth. 1985. Lordosis in *Gila*, Yampa River, Colorado. Proc. Desert Fish. Counc. 13-15 A: 83–84.

Haynes, C. M., and J. R. Bennett. 1986. The relationship between the preservation of wilderness values and endangered species: a case-study from the Upper Colorado River Basin, U.S.A., p. 188–196. *In* R. C. Lucas, compiler. Proceedings — National Wilderness Research Conference: Current Research. US Forest Service Gen. Tech. Rep. INT-212.

Hely, A. G., 1969. Lower Colorado River water supply — its magnitude and distribution. US Geol. Surv. Prof. Pap. 486-D: 54 p.

Hickman, T. J. 1983. Effects of habitat alteration by energy resource development in the Upper Colorado River Basin on endemic fishes, p. 537-550. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbour, MI.

Holden, P. B. 1979. Ecology of riverine fishes in regulated stream systems with emphasis on the Colorado River, p. 57–74. *In* J. V. Ward and J. A. Stanford [ed.] The ecology of regulated streams. Plenum, New York, NY.

Holden, P. B., and C. B. Stalnaker. 1975. Distribution and abundance of mainstem fishes of the Middle and Upper Colorado River Basins, 1967–73. Trans. Am. Fish. Soc. 104: 217–231.

Howard, A. D., and R. Dolan. 1981. Geomorphology of the Colorado River in the Grand Canyon. J. Geol. 89: 269–298.

Hubbard, J. P. 1980. The impacts of habitat alterations and introduced species on the native fishes of the Upper Colorado River Basin: a discussion, p. 182–192. *In* W. O. Spofford, A. L. Parker, and A. V. Kneese [ed.] Energy development in the Southwest — problems of water, fish and wildlife in the Upper Colorado River Basin, vol. 2. Resources for the Future, Washington, D.C.

Hubbs, C. L. 1953. *Eleotris picta* added to the fish fauna of California. Calif. Fish Game 39: 69–76.

Hubbs, C. L., and R. R. Miller. 1948. Correlation between fish distribution and hydrographic history in the desert basins of western United States. Bull. Univ. Utah 38: 17–114.

Hughes, J. D. 1967. The story of man at Grand Canyon. Grand Canyon Nat. History Assoc. Bull. 14: 195 p.

Hundley, N. 1966. Dividing the waters. University of California Press, Berkeley, CA. 266 p.

Hundley, N. 1986. The West against itself: the Colorado River — an institutional history, p. 9–49. *In* G. D. Weatherford and F. L. Brown [ed.] New courses for the Colorado River — major issues for the next century. University of New Mexico Press, Albuquerque, NM.

Hunt, C. B. 1974. Natural regions of the United States and Canada. Freeman, San Francisco, CA. 725 p.

Inhat, J. M., and R. V. Bulkley. 1984. Influence of acclimation temperature and season on acute temperature preference of adult mountain whitefish, *Prosopium williamsoni*. Environ. Biol. Fish. 11: 29–40.

Iorns, W. V., C. H. Hembree, and G. L. Oakland. 1965. Water resources of the Upper Colorado River Basin — technical report. US Geol. Surv. Prof. Pap. 441: 370 p.

Jacobsen, R. D. 1982. New impacts by man in the Upper Colorado River Basin, p. 71–80. *In* W. H. Miller, H. M. Tyus, and C. A. Carlson [ed.] Fishes of the Upper Colorado River system: present and future. Western Division, American Fisheries Society, Bethesda, MD.

Johnson, J. E. 1970. Age, growth, and population dynamics of threadfin shad, *Dorosoma petenense* (Gunther), in central Arizona reservoirs. Trans. Am. Fish. Soc. 99: 739–753.

1971. Maturity and fecundity of threadfin shad, *Dorosoma petenense* (Gunther), in central Arizona reservoirs. Trans. Am. Fish. Soc. 100: 74–85.

1985. Reintroducing the natives: razorback sucker. Proc. Desert Fish. Counc. 13: 73–79.

1987. Protected fishes of the United States and Canada. Fisheries. American Fisheries Society, Bethesda, MD. 42 p.

Johnson, J. E., and J. N. Rinne. 1982. The Endangered Species Act and Southwest fishes. Fisheries 7(3): 2–8.

Johnson, R. R., and D. A. Jones [tech. coord.] 1977. Importance, preservation and management of riparian habitats: a symposium. Gen. Tech. Rep. RM-43, Rocky Mt. For. Range Exp. Sta., Ft. Collins. CO. 217 p.

Jones, R. L., and H. M. Tyus. 1985. Recruitment of Colorado squawfish in the Green River Basin, Colorado and Utah 1979–1984. US Fish and Wildlife Service, Region 6, Denver, CO. 24 p. (Available from US Fish and Wildlife Service, P.O. Box 25486, Denver Federal Center, Denver, CO 80225)

Joseph, T. W., J. A. Sinning, R. J. Behnke, and P. B. Holden. 1977. An evaluation of the status, life history, and habitat requirements of endangered and threatened fishes of the Upper Colorado River System. US Fish Wildl. Serv. FWS/OBS-77/62. 169 p.

Kaeding, L. R., and M. A. Zimmerman. 1983. Life history and ecology of the humpback chub in the Little Colorado and Colorado rivers of Grand Canyon. Trans. Am. Fish. Soc. 112: 577–594.

Koster, W. J. 1957. Guide to the fishes of New Mexico. University of New Mexico Press, Albuquerque, NM. 116 p.

LaRue, E. C. 1916. Colorado River and its utilization. US Geol. Surv. Water Supply Pap. 395: 231 p.

Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. 1980. Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh, NC. 854 p.

Marsh, P. C. 1985. Effect of incubation temperatures on survival of embryos of native Colorado River fishes. Southwest. Nat. 30: 129–140.

Marsh, P. C. 1987. Digestive tract contents of adult razorback suckers in Lake Mohave, Arizona-Nevada. Trans. Am. Fish. Soc. 116: 117–119.

Marsh, P. C., and W. E. Rinne. 1983. An unusally [sic] high incidence of spinal deformity among threadfin shed. Southwest. Nat. 28: 117–118.

Martin, W. E., E. H. Bollman, and R. L. Gum. 1982. Economic value of the Lake Mead fishery. Fisheries 7(6): 20–24

Masse, W. B. 1981. Prehistoric irrigation systems in the Salt River Valley, Arizona. Science 214: 408–415.

McAda, C. W. 1983. Colorado squawfish, *Ptychocheilus lucius* (Cyprinidae), with a channel catfish, *Ictalurus punctatus* (Ictaluridae), lodged in its throat. Southwest. Nat. 28: 119–120.

McAda, C. W., and R. W. Wydoski. 1983. Maturity and fecundity of the bluehead sucker, *Catostomus discobolus* (Catostomidae), in the Upper Colorado River Basin, 1975–76. Southwest. Nat. 28: 120–123.

1985. Growth and reproduction of the flannelmouth sucker, *Catostomus latipinnis*, in the Upper Colorado River Basin, 1975–76. Great Basin Nat. 45: 281–286.

Meffe, G. K. 1983. Attempted chemical renovation of an Arizona spring brook for management of the endangered Sonoran topminnow. N. Am. J. Fish. Manag. 3: 315–321.

1984. Effects of abiotic disturbance on coexistence of predatory-prey fish species. Ecology 65: 1525–1534.

1985. Predation and species replacement in American southwestern fishes: a case study. Southwest Nat. 30: 173–187.

1986. Conservation genetics and the management of endangered fishes. Fisheries 11(1): 14–23.

Meffe, G. K., D. A. Hendrickson, W. L. Minckley, and J. N. Rinne. 1983. Factors resulting in decline of the endangered Sonoran topminnow *Poeciliopsis occidentalis* (Atheriniformes: Poeciliidae) in the United States. Biol. Conserv. 25: 135–159.

Miller, J. B., D. L. Wegner, and D. R. Bruemmer. 1983. Salinity and phosphorus routing through the Colorado River/reservoir system, p. 19–41. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI.

Miller, R. R. 1943. The status of *Cyprinodon macularius* and *Cyprinodon nevadensis*, two desert fishes of western North America. Occ. Pap. Mus. Zool. Univ. Mich. 473: 1–25.

1959. Origin and affinities of the freshwater fish fauna of western North America, p. 187–222. *In* C. L. Hubbs [ed.] Zoogeography. Am. Assoc. Adv. Sci. Publ. 51: 509 p.

1961. Man and the changing fish fauna of the American Southwest. Pap. Mich. Acad. Sci. Arts. Lett. 46: 365–404.

1963. Is our native underwater life worth saving? Nat.

Parks Mag. 1963.

1972. Threatened freshwater fishes of the United States. Trans. Am. Fish. Soc. 101: 239–252.

1981. Coevolution of desert and pupfishes (genus *Cyprinodon*) in the American Southwest, p. 39–94. *In* R. J. Naiman and D. L. Soltz [ed.] Fishes in North American deserts. J. Wiley and Sons, New York, NY.

Miller, R. R., and C. H. Lowe. 1964. An annotated check list of the fishes of Arizona, p. 133–151. *In* C. H. Lowe [ed.] The vertebrates of Arizona. University of Arizona Press, Tucson, AZ.

Miller, W. H., H. M. Tyus, and C. A. Carlson [ed.] 1982a. Fishes of the Upper Colorado River System: present and future. Western Division, American Fisheries Society, Bethesda, MD. 131 p.

Miller, W. H., J. J. Valentine, D. L. Archer, H. M. Tyus, R. A. Valdez, and L. R. Kaeding [ed.]. 1982b. Colorado River Fisheries Project, Part 1. Summary report. US Bureau of Reclamation, Salt Lake City, UT. 42 p. (Available from US Bureau of Reclamation, Upper Colorado Regional Office, P.O. Box 11568, Salt Lake City, UT 84147)

1982c. Colorado River Fisheries Project, Part 2. Field investigations. US Bureau of Reclamation, Salt Lake City, UT. 365 p. (Available from US Bureau of Reclamation, Upper Colorado Regional Office, P.O. Box 11568, Salt Lake City, UT 84147)

1982d. Colorado River Fisheries Project, Part 3. Contracted studies. US Bureau of Reclamation, Salt Lake City, UT. 324 p. (Available from US Bureau of Reclamation, Upper Colorado Regional Office, P.O. Box 11568, Salt Lake City, UT 84147)

Minckley. W. L. 1973. Fishes of Arizona. Arizona Game and Fish Department, Phoenix, AZ. 393 p.

1979. Aquatic habitats and fishes of the lower Colorado River, southwestern United States. US Bureau of Reclamation, Boulder City, NV. 478 p. (Available from US Bureau of Reclamation, Lower Colorado Regional Office, P.O. Box 427, Boulder City, NV 89005)

1983. Status of the razorback sucker, *Xyrauchen texanus* (Abbott) in the Lower Colorado River Basin. Southwest. Nat. 28: 165–187.

Minckley, W. L., J. N. Rinne, and J. E. Johnson. 1977. Status of the Gila topminnow and its co-occurrence with mosquitofish. US For. Serv. Res. Pap. RM-198: 1–8.

Minckley, W. L., D. A. Hendrickson, and C. E. Bond. 1986. Geography of western North American freshwater fishes; description and relations to intracontinental tectonism, p. 519–613. *In* C. H. Hocutt and E. O. Wiley [ed.] Zoogeography of North American freshwater fishes. John Wiley and Sons, New York, NY.

Minshall, G. W., K. W. Cummins, R. C. Peterson, C. E. Cushing, D. A. Bruns, J. A. Sedell, and R. L. Vannote. 1985. Developments in stream ecosystem theory. Can. J. Fish. Aquat. Sci. 42: 1045–1055.

Moffett, J. W. 1942. A fishery survey of the lower Colorado River below Boulder Dam. Calif. Fish Game 28: 76–86.

1943. A preliminary report on the fishery of Lake Mead. Trans. N. Am. Wildl. Conf. 1943: 179–186.

Molles, M. 1980. The impacts of habitat alterations and introduced species on the native fishes of the Upper Colorado River Basin, p. 163–181. *In* W. O. Spofford, A. L. Parker, and A. V. Kneese [ed.] Energy development in the Southwest — problems of water, fish and wildlife in the Upper Colorado River Basin, vol. 2. Resources for the Future, Washington, D.C.

Morgensen, S. A. 1983. The effects of water level fluctuations on the spawning success of largemouth bass in Lake Mead, p. 563–578. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI.

Moyle, P. B. 1976. Inland fishes of California. University of California Press, Berkeley, CA. 405 p.

Mullan, J. W., V. J. Strarostka, D. John, J. L. Stone, R. W. Wiley, and W. J. Wiltzius. 1976. Factors affecting Upper Colorado River reservoir tailwater trout fisheries, p. 405–427. *In* J. F. Orsborn, and C. H. Allman [ed.] Proceedings, symposium and specialty conference, instream flow needs, vol 2. American Fisheries Society, Bethesda, MD.

Muth, R. T., C.M. Haynes, and C. A. Carlson. 1985. Culture of roundtail chub, *Gila robusta robusta* (Cyprinidae), through the larval period. Southwest. Nat. 30: 152–154.

Muth, R. T., T. P. Nesler, and A. F. Wasowicz. 1988. Marking cyprinid larvae with tetracycline. Am. Fish. Soc. Symp. 5: 89–95.

Nash, R. 1970. Grand Canyon of the living Colorado. Sierra Club and Ballantine Books, New York, NY. 143 p.

1986. Wilderness values and the Colorado River, p. 201–214. *In* G. D. Weatherford and F. L. Brown [ed.] New courses for the Colorado River — major issues for the next century. University of New Mexico Press, Albuquerque, NM.

Nesler, T. P., R. T. Muth, and A.F. Wasowicz. 1988. Evidence for baseline flow spikes as spawning cues for Colorado squawfish in the Yampa River, Colorado. Am. Fish. Soc. Symp. 5: 68–79.

Ohmart, R. D., W. O. Deason, and C. Burke. 1977. A riparian case history: the Colorado River, p. 35–47. *In* R. R. Johnson, and D. A. Jones [tech. coord.] Importance, preservation and management of riparian habitats: a symposium. Gen. Tech. Rep. RM-43, Rocky Mt. For. Range Exp. Sta., Ft. Collins, CO.

Parenti, L. R. 1981. A phylogenetic and biogeographic analysis of cyprinodontiform fishes (Teleostei, Antherinomorpha). Bull. Am. Mus. Nat. Hist. 168: 335–357.

Paulson, L. J. 1983. Use of hydroelectric dams to control evaporation and salinity in the Colorado River System, p. 439–456. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI.

Paulson, L. J., and J. R. Baker. 1983. The effects of impoundments on salinity in the Colorado River, p. 457–474. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI.

Pearson, W. D., R. H. Kramer, and D. R. Franklin. 1968. Macroinvertebrates in the Green River below Flaming Gorge Dam, 1964–65 and 1967. Proc. Utah Acad. Sci., Arts, Lett. 45: 148–167.

Persons, W. R., and R. V. Bulkley. 1982. Feeding activity and spawning time of striped bass in the Colorado River inlet, Lake Powell, Utah. N. Am. J. Fish. Manage. 4: 403–408.

Petts, G. E. 1984. Impounded rivers — perspectives for ecological management. Wiley, New York, NY. 326 p.

Pillsbury, A. F. 1981. The salinity of rivers. Sci. Am. 245: 55–65.

Pimentel, R., R. V. Bulkley, and H. M. Tyus. 1985. Choking of Colorado squawfish, *Ptychocheilus lucius* (Cyprinidae), on channel catfish, *Ictalurus punctatus* (Ictaluridae), as a cause of mortality. Southwest. Nat. 30: 154–158.

Pister, E. P. 1981. Conservation of desert fishes, p. 411–445. *In* R. J. Naiman and D. L. Soltz [ed.] Fishes in North American deserts. J. Wiley and Sons, New York, NY.

Plummer, B. 1983. The Colorado, a river for many people, p. 3–12. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI.

Prentki, R. T., and L. J. Paulson. 1983. Historic patterns of phytoplankton productivity in Lake Mead, p. 105–123. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI.

Regier, H. A., R. L. Welcomme, R. J. Steedman, and H. F. Henderson. 1989. Rehabilitation of degraded river ecosystems. p. 86-97. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Rinne, J. N. 1976. Cyprinid fishes of the genus *Gila* from the lower Colorado River Basin. Wass. J. Biol. 34: 65–107.

Rinne, J. N., and W. L. Minckley. 1970. Native Arizona fishes, Part III — the minnows called "chubs." Wildl. Views 17: 12–19.

Robins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada. Am. Fish. Soc. Spec. Publ. 12: 174 p.

Scarnecchia, D. L., and E. P. Bergersen. 1986. Production and habitat of threatened greenback and Colorado River cutthroat trouts in Rocky Mountain headwater streams. Trans. Am. Fish. Soc. 115: 382–391.

Schoenherr, A. A. 1981. The role of competition in the replacement of native species by introduced fishes, p. 173–203. *In* R. J. Naiman and D. L. Soltz [ed.] Fishes in North American Deserts. J. Wiley and Sons, New York, NY.

Sigler, W. F., and R. R. Miller. 1963. Fishes of Utah. Utah Department of Fish and Game, Salt Lake City, UT. 203 p.

Smith, G. R. 1966. Distribution and evolution of The North American catostomid fishes of the subgenus *Pantosteus*, genus *Catostomus*. Misc. Publ. Mus. Zool. Univ. Mich. 129: 1–132.

1978. Biogeography of intermountain fishes, p. 17–42. *In* K. T. Harper and J. L. Reveal [ed.] Intermountain biogeography: a symposium. Great Basin Nat. Mem. 2: 268 p.

Snyder, D. E. 1981. Contributions to a guide to the cypriniform fish larvae of the Upper Colorado River System in Colorado. Colo. Office, US Bur. Land Manage. Bio. Sci. Ser. 3: 81 p.

Spofford, W. O. 1980. Potential impacts of energy development on stream flows in the Upper Colorado River Basin, p. 351–429. *In* W. O. Spofford, A. L. Parker, and A. V. Kneese [ed.] Energy development in the Southwest — problems of water, fish and wildlife in the Upper Colorado River Basin, vol. 1. Resources for the Future, Washington, DC.

Spofford, W. O., A. L. Parker, and A. V. Kneese. [ed.] 1980. Energy development in the Southwest — problems of water, fish and wildlife in the Upper Colorado River Basin, 2 vols. Resources for the Future, Washington, D.C. 523; 543 p.

Stanford, J. A., and J. V. Ward. 1983. The effects of mainstream dams on physicochemistry of the Gunnison River, Colorado, p. 43–56. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI.

1986a. The Colorado River System, p. 353–374. *In* B. R. Davies and K. F. Walker [ed.] The ecology of river systems. Dr. W. Junk, Dordrecht, The Netherlands.

1986b. Reservoirs of the Colorado system, p. 375–383. *In* B. R. Davies and K. F. Walker [ed.] The ecology of river systems. Dr. W. Junk, Dordrecht, The Netherlands.

1986c. Fishes of the Colorado system, p. 385–402. *In* B. R. Davies and K. F. Walker [ed.] The ecology of river systems. Dr. W. Junk, Dordrecht, The Netherlands.

Stegner, W. 1982. Beyond the hundredth meridian — John Wesley Powell and the second opening of the West. University of Nebraska Press, Lincoln, NE. 438 p.

Sykes, G. 1937. The Colorado delta. Am. Geogr. Soc. Spec. Publ. 19: 193 p.

Turner, R. M., and M. M. Karpiscak. 1980. Recent vegetation changes along the Colorado River between Glen Canyon Dam and Lake Mead, Arizona. US Geol. Surv. Prof. Pap. 1132: 125 p.

Tyus, H. M. 1984. Loss of stream passage as a factor in the decline of the endangered Colorado squawfish, p. 138–144. *In* Issues and technology in the management of impacted western wildlife, proceedings of a national symposium. Thorne Ecol. Inst. Tech. Publ. 14. Boulder, CO. (Available from US Fish and Wildlife Service, P.O. Box 25426, Denver Federal Center, Denver, CO 80225)

1985. Homing behavior noted for Colorado squawfish. Copeia 1985: 213–215.

1987. Distribution, reproduction, and habitat use of the razorback sucker in the Green River, Utah, 1979–1986. Trans. Am. Fish. Soc. 116: 111–116.

Tyus H. M., B. D. Burdick, R. A. Valdez, C. M. Haynes, T. A. Lytle, and C. R. Berry. 1982. Fishes of the Upper Colorado River Basin: abundance and status, p. 12–70. *In* W. H. Miller, H. M. Tyus, and C. A. Carlson [ed.] Fishes of the Upper Colorado River System: present and future. Western Division, American Fisheries Society, Bethesda, MD.

Tyus, H. M., and C. W. McAda. 1984. Migration, movements and habitat preferences of Colorado squawfish, *Ptychocheilus lucius*, in the Green, White and Yampa rivers, Colorado and Utah. Southwest. Nat. 29: 289–299.

Tyus, H. M., B. D. Burdick, and C. W. McAda. 1984. Use of radiotelemetry for obtaining habitat preference data on Colorado squawfish. N. Am. J. Fish. Manage. 4: 177–180.

Upper Colorado River Commission. 1984. Thirty sixth Annual Report. Salt Lake City, UT. 87 p.

U.S. Department of the Interior. 1982. Endangered and threatened wildlife and plants; review of vertebrate wildlife for listing as endangered or threatened species. Fed. Reg. 47: 58455–58460.

1983. Republication of the lists of endangered and threatened species; final rule. Fed. Reg. 48: 34182–34196.

1985a. Endangered and threatened wildlife and plants; proposal to determine the spikedace to be a threatened species. Fed. Reg. 50: 25390–25398.

1985b. Endangered and threatened wildlife and plants; proposal to determine *Lepidomeda vittata* (Little Colorado spinedace) to be a threatened species. Fed. Reg. 50: 21095–21103.

1985c. Endangered and threatened wildlife and plants; proposal to determine the loach minnow to be a threatened species. Fed. Reg. 50: 25380–25387.

1985d. Endangered and threatened wildlife and plants; notice of completion of review for species listed before 1976 and in 1979 and 1980. Fed. Reg. 50: 29900–29909.

1985e. Endangered and threatened wildlife and plants; review of vertebrate wildlife; notice of review. Fed. Reg. 50: 37958–37962.

1986a. Intent to prepare an environmental assessment on a proposed action to recover rare and endangered fish in the Upper Colorado River Basin; republication. Fed. Reg. 51: 28891–28894.

1986b. Endangered and threatened wildlife and plants; determination of endangered status and critical habitat for the desert pupfish. Fed. Reg. 51: 10842–10851.

1986c. Endangered and threatened wildlife and plants; determination of threatened status and critical habitat for the Railroad Valley springfish. Fed. Reg. 51: 10857–10865.

1986d. Endangered and threatened wildlife and plants; proposed listing of Virgin River chub as an endangered species with critical habitat. Fed. Reg. 51: 22949–22955.

1986e. Endangered and threatened wildlife and plants; determination of threatened status for the spikedace. Fed. Reg. 51: 23769–23781.

1987. Endangered and threatened wildlife and plants, 50 CFR 17.11 and 17.12. U.S. Government Printing Office, Washington, DC.

U.S. GEOLOGICAL SURVEY. 1975. Surface water supply of the United States, 1966–70, part 9. Colorado River Basin, vol. 3. Lower Colorado River Basin. US Geol. Surv. Water-Supply Pap. 2126: 681 p.

VALDEZ, R. A., AND E. J. WICK. 1983. Natural vs manmade backwaters as native fish habitat, p. 519–536. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI.

VALENTINE, V. E. 1983. Institutional perspectives on Colorado River management, p. 667–672. *In* V. D. Adams and V. A. Lamarra [ed.] Aquatic resources management of the Colorado River ecosystem. Ann Arbor Science Publishers, Ann Arbor, MI.

VRIJENHOEK, R. C., M. E. DOUGLAS, AND G. K. MEFFE. 1985. Conservation genetics of endangered fish populations in Arizona. Science 229: 400–402.

WALLIS, O. L. 1951. The status of the fish fauna of the Lake Mead National Recreation Area, Arizona-Nevada. Trans. Am. Fish. Soc. 80: 84–92.

WARD, J. V., AND J. A. STANFORD. 1983. The regulated stream as a testing ground for ecological theory, p. 23–38. *In* A. Lillehammer and S. J. Saltveit [ed.] Regulated rivers. Oslo Univ. Press, Oslo, Norway.

WARD, J. V., H. J. ZIMMERMANN, AND L. D. CLINE. 1986. Lotic zoobenthos of the Colorado system, p. 403–422. *In* B. R. Davies and K. F. Walker [ed.] The ecology of river systems. Dr. W. Junk, Dordrecht, The Netherlands.

WATKINS, T. H. [ed.] 1969. The grand Colorado. American West Publishing Co., Palo Alto, CA. 310 p.

WEATHERFORD, G. D., AND G. C. JACOBY. 1975. Impact of energy development on the law of the Colorado River. Nat. Resour. J. 15: 171–213.

WEATHERFORD, G. D., AND F. L. BROWN. 1986. Introduction: a timely look at a timeless river, p. 1–7. *In* G. D. Weatherford and F. L. Brown [ed.] New courses for the Colorado River — major issues for the next century. University of New Mexico Press, Albuquerque, NM.

WELSH, F. 1985. How to create a water crisis. Johnson Publishing Co., Boulder, CO. 238 p.

WHITE, G. F. 1986. A new confluence in the life of the river, p. 215–224. *In* G. D. Weatherford and F. L. Brown [ed.] New courses for the Colorado River — major issues for the next century. University of New Mexico Press, Albuquerque, NM.

WICK, E. J., J. A. HAWKINS, AND C. A. CARLSON. 1985. Colorado squawfish and humpback chub population and habitat monitoring, 1983–1984. Colo. Div. Wildl. End. Wildl. Invest. Final Rept. SE 3–7: 48 p. (Available from Colorado Division of Wildlife, 6060 Broadway, Denver, CO 80216)

WILLIAMS, J. E., D. B. BOWMAN, J. E. BROOKS, A. A. ECHELLE, R. J. EDWARDS, D. A. HENDRICKSON, AND J. L. LANDYE. 1985. Endangered aquatic ecosystems in North American deserts with a list of vanishing fishes of the region. J. Ariz.-Nev. Acad. Sci. 20: 1–62.

WOODWARD, D. F., R. G. RILEY, M. G. HENRY, J. S. MEYER, AND T. R. GARLAND. 1985. Leaching of retorted oil shale: assessing the toxicity to Colorado squawfish, fathead minnows, and two food-chain organisms. Trans. Am. Fish. Soc. 114: 887–894.

Hydrological, Morphometrical, and Biological Characteristics of the Connecting Rivers of the International Great Lakes: A Review[1]

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Abstract

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The connecting channels of the Great Lakes are large rivers (1 200–9 900 $m^3 \cdot s^{-1}$) with limited tributary drainage systems and relatively stable hydrology (about 2:1 ratio of maximum to minimum flow). The rivers, from headwaters to outlet, are the St. Marys, St. Clair, Detroit, Niagara, and St. Lawrence. They share several characteristics with certain other large rivers: the fish stocks that historically congregated for spawning or feeding have been overfished, extensive channel modifications have been made, and they have been used as a repository for domestic and industrial wastes and for hydroelectric energy generation. Levels of phosphorus, chlorophyll *a*, and particulate organic matter increase 3- to 5-fold from the St. Marys River to the St. Lawrence River. Biological communities dependent on nutrients in the water column, such as phytoplankton, periphyton, and zooplankton similarly increase progressively downstream through the system. The standing crop of emergent macrophytes is similar in all of the rivers, reflecting the relatively large nutrient pools in the sediments and atmosphere. Consequently, emergent macrophytes are an important source of organic matter (67 % of total primary production) in the nutrient poor waters of the St. Marys River, whereas phytoplankton production dominates (76 %) in the enriched St. Lawrence River. Submersed and emergent macrophytes and the associated periphyton are major producers of organic matter in the connecting channels. Another major source of organic matter (measured as ash free dry weight, AFDW) in the Detroit River is sewage, introduced at a rate of 26 000 t per year. The production of benthos ranges from a low of 5.4 g AFDW$\cdot m^{-2}$ in the Detroit River to a high of 15.5 g AFDW$\cdot m^{-2}$ in the St. Marys River. The rivers lack the organic transport from riparian sources upstream but receive large amounts of high quality phytoplankton and zooplankton from the Great Lakes.

Résumé

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Les voies qui relient les Grands Lacs sont d'importants cours d'eau (1 200 à 9 900 $m^3 \cdot s^{-1}$) dont les bassins de drainage comptent un nombre limité de tributaires et dont l'hydrologie est relativement stable (rapport d'environ 2:1 du débit maximal au débit minimal). Les cours d'eau, depuis les eaux d'amont jusqu'à l'effluent, sont les rivières St. Marys, St. Clair, Détroit, Niagara et le fleuve Saint-Laurent. Ils partagent plusieurs caractéristiques avec certains autres grands cours d'eau : les stocks de poisson qui par le passé se rassemblaient pour frayer ou pour s'alimenter ont été surexploités, d'importantes modifications ont été apportées aux voies d'eau et elles ont été utilisées comme endroits de rejet des déchets domestiques et industriels et pour la production d'énergie hydro-électrique. Les concentrations de phosphore, de chlorophylle *a* et de matière organique particulaire s'accroissent de 3 à 5 fois entre la rivière St. Marys et le fleuve Saint-Laurent. De la même façon, les communautés biologiques qui dépendent des substances nutritives présentes dans la colonne d'eau comme le phytoplancton, le périphyton et le zooplancton augmentent progressivement vers l'aval dans tout le système. La biomasse des macrophytes émergés est semblable dans tous les cours d'eau, ce qui reflète les concentrations relativement importantes de substances nutritives dans les sédiments et dans l'atmosphère. Par conséquent, les macrophytes émergés constituent une source importante de matière organique (67 % de toute la production primaire) dans les eaux pauvres en substances nutritives de la rivière St. Marys, tandis que la production de phytoplancton domine (76 %) dans les eaux enrichies du fleuve Saint-Laurent. Les macrophytes immergés et émergés de même que le périphyton qui leur est associé sont d'importants producteurs de matière organique dans les voies de communication. Une autre source importante de matière organique (mesurée en poids sec sans cendre, PSSC) dans la rivière Détroit est constituée par les eaux usées, qui sont déversées à un rythme de 26 000 t par année. La production de benthos varie d'une faible valeur de 5,4 g PSSC$\cdot m^{-2}$ dans la rivière Détroit à un maximum de 15,5 g PSSC$\cdot m^{-2}$ dans la rivière St. Marys. Les cours d'eau ne profitent pas du transport de la matière organique de sources riveraines en amont, mais reçoivent des Grands Lacs de grandes quantités de phytoplancton et de zooplancton de haute qualité.

Introduction

The Laurentian Great Lakes, which compose the largest freshwater system in the world, represent a unique ecosystem. Joining these large lakes and connecting them with the Atlantic Ocean are a set of little-studied rivers, frequently referred to as connecting channels (here called connecting rivers). The rivers from headwaters to outlet are; St. Marys, St. Clair, Detroit, Niagara, and the St. Lawrence. The connecting rivers have some unusual morphometric and hydrologic characteristics but, like many other rivers, have been subjected to various perturbations. The rivers have at least three unique attributes: (1) flows that vary considerably less than those in most rivers of similar size, (2) a limited tributary drainage system (consequently most stream ordering systems are not applicable), and (3) headwaters (i.e., the Great Lakes) that are relatively unpolluted — i.e., each river begins in a mature and non-degraded state. Like other large rivers of the world, these connecting rivers have been subjected to several perturbations: (a) overfishing of fish stocks that historically congregated for spawning or feeding or completed their entire life cycle in the rivers, (b) the removal of impediments to navigation through channel modification, (c) the influence of domestic and industrial waste products, and (d) the development of hydroelectric energy. The St. Marys River, which is the least influenced by these changes (except for navigation channels and localized pollution), has a shoreline and littoral zone essentially unchanged from that present before European settlement. The Detroit and Niagara rivers are probably influenced most by human activities.

Our purpose here is to provide an overview of the morphology, hydrology, and biology of four of these rivers. Although few biological data have been collected in the fifth — the Niagara River — we include hydrological data for comparison. We also attempt to identify and estimate the effects of the changes resulting from human efforts to modify these rivers to meet the needs of commerce and industry. In the following text we treat each "category of material" from upstream to downstream — primarily from the St. Marys River to the St. Clair–Detroit River system (SCDRS), to the St. Lawrence River.

Geology

The rock strata underlying the connecting rivers range in age from Precambrian to Holocene or Recent. Surface bedrock is made up predominantly of Silurian and Devonian marine deposits that consist of dolomite and limestone in the St. Marys, Detroit, and Niagara rivers and shales in the St. Clair River, Lake St. Clair, and the St. Lawrence River (Hough 1958). More subtle topographic features are results of glacial scour and filling during the Pleistocene. The retreat and intermittent re-advance of ice during Wisconsin glaciation 10 000–14 000 years ago caused marked changed in Great Lakes water levels, altered discharge routes from the lakes, and greatly influenced the distribution of fishes in the region (Bailey and Smith 1981).

Hydrology and Morphometry

Each of the connecting rivers is the single natural outlet of the Great Lake immediately upstream. As the land area and lake surface contributing to the watershed increase downstream, from Lake Superior through Lakes Huron, Michigan, Erie, and Ontario, discharge likewise increases progressively, from the St. Marys River to the St. Lawrence River (Table 1). The most northerly of the connecting rivers, the St. Marys, flows southwesterly from Whitefish Bay, Lake Superior, into Lake Huron at De Tour, Michigan (Fig. 1). Most of the 6.7 m drop in elevation of the river is at the St. Marys Rapids, a 1.6 km wide reach between Sault Ste. Marie, Michigan and Ontario. Below these rapids the river splits into several channels and broadens to form Lakes George and Nicolet (Fig. 1). Several large embayments, Lake Munuscong and Potagannissing Bay, adjoin the main stem of the lower river. Water currents may reach 1.0 $m \cdot s^{-1}$ in narrow constricted channels, but are characteristically 0.2–0.5 $m \cdot s^{-1}$ and may be negligible in emergent wetlands bordering the river.

The SCDRS flows in a southerly direction about 143 km from Lake Huron into Lake Erie (Fig. 1). The St. Clair River is bordered by an industrial corridor in the north and empties into Lake St. Clair through a large delta consisting of three main channels and a number of secondary channels. Lake St. Clair has a surface area of 1 114-km^2, a mean depth of 3.4 m, and a maximum depth of 6.4 m. The Detroit River flows south from Lake St. Clair and also separates into several channels before emptying into Lake Erie. The width of the SCDRS ranges from 250 m in the Upper St. Clair River to 3 000 m in the lower Detroit River. Average water velocities range from 0.6–1.8 $m \cdot s^{-1}$ in the mid-channel region to 0.1–0.9 $m \cdot s^{-1}$ in nearshore and near-channel areas. Average flushing times are 21 h for the St. Clair River, 5–7 d for Lake St. Clair, and 19 h for the Detroit River. Mean annual flow, as well as monthly ranges in flow, in the SCDRS are about double the flow in the St. Marys River (Table 1). More detailed information on physical characteristics of the SCDRS was given by Hudson et al. (1986) and Derecki (1984a, b, c; 1985).

The Niagara River flows northerly from Lake Erie at Buffalo, New York, to Lake Ontario at Niagara-on-the-Lake, Ontario (Fig. 1). Within the river's 58 km course, it drops almost 100 m in elevation (Table 1). About half of this drop (56 m) occurs as the river cascades over the Niagara Escarpment at Niagara Falls, which separates the upper and lower reaches of the river (Fig. 1).

The St. Lawrence River is the outlet of Lake Ontario; from its origin at Wolfe Island/Tibbetts Point, it flows northeast to the Gulf of St. Lawrence. The St. Lawrence River is the longest of the connecting rivers (Table 1). It forms the international border between Canada and the United States along the first 182 km of its course, then enters the Province of Quebec. The area of the river's drainage basin along the international section is only 18 726 km^2 — or roughly 2.5% of its cumulative Great Lakes drainage basin (Table 1). At 1987 water levels (about 1 m above mean low water datum), the surface area of the international section of the river is 655 km^2, the mean depth is 9.5 m, and average flushing time is 10.7 d (range, 7.3–16.5 d).

The St. Lawrence River descends about 74 m over its entire course, about one-third of this descent being its international section (Fig. 1). The international section may be separated into three reaches on the basis of limnological characteristics: The upper reach, which has numerous islands, expansive bays, and shoals, is most influenced by Lake Ontario, and behaves essentially as an extension of the lake. The middle reach is narrow and has few islands or shoals, except for several large islands in the stretch between Ogdensburg, New York, and Cardinal, Ontario; this middle reach culminates at Red Mills Rapids (Fig. 1). The lower reach of the river, now known as Lake St. Lawrence, is highly modified and contains several large islands and extensive shoals, many of which are remnants of inundated islands.

Anthropogenic Changes

Each connecting river of the Great Lakes has been modified to accommodate shipping from the Atlantic Ocean to the interior of North America, as well as among lakes; however, shipping bypasses the Niagara River through the Welland Canal (Fig. 1). Hydroelectric generating facilities have been constructed on the St. Marys, Niagara, and St. Lawrence rivers.

The first navigation locks in the Great Lakes system were

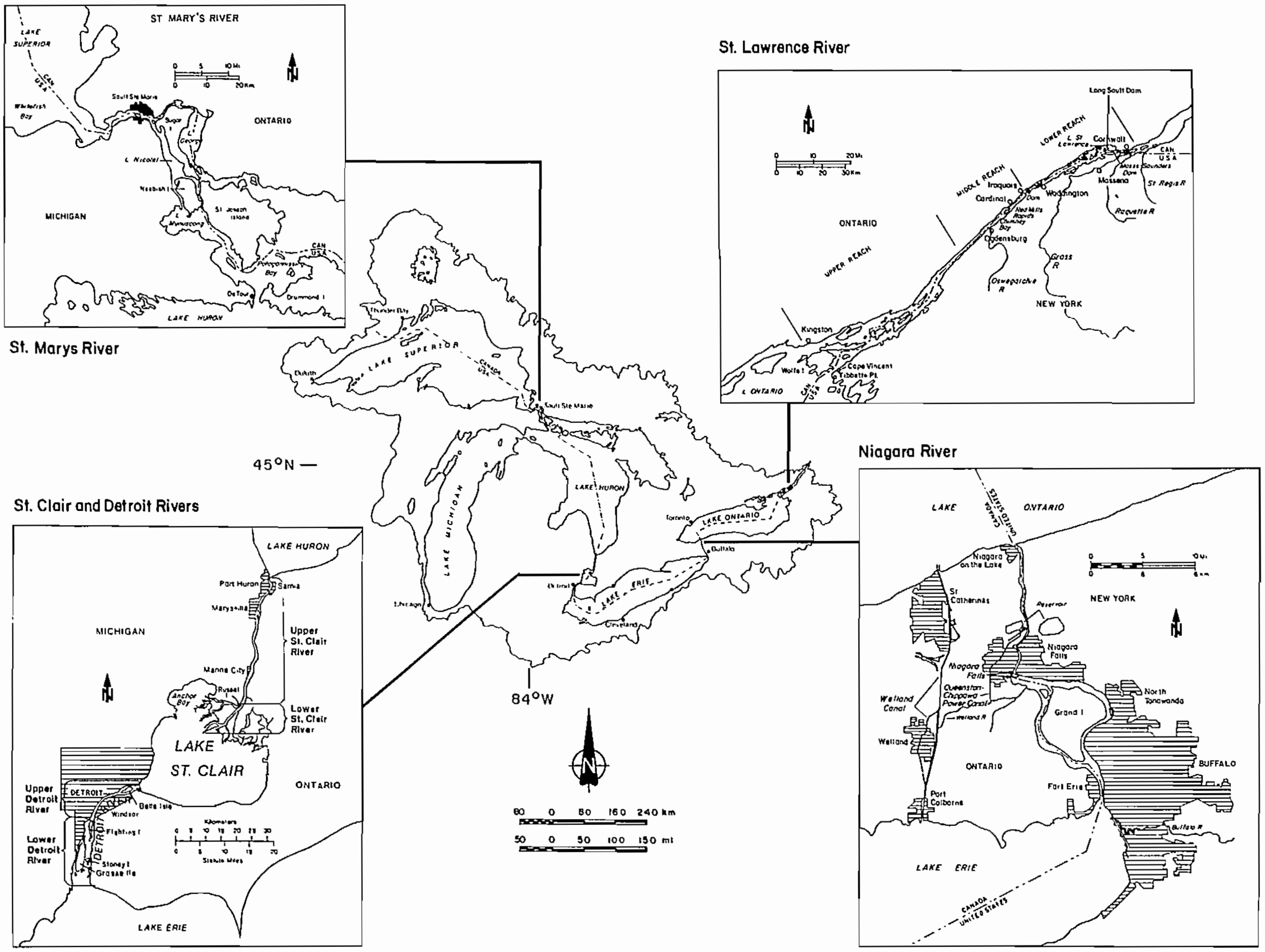

FIG. 1. Great Lakes Watershed and the five connecting channels.

constructed on the St. Lawrence River in 1783, between Lakes St. Francis and St. Louis, Quebec. The Erie and Welland canals, completed in 1825 and 1829, respectively, enabled vessels to reach Lake Erie. Several canals 3 m deep had also been completed in the St. Lawrence River by 1847, allowing barge and boat traffic to reach Lake Ontario. The upper Great Lakes were opened to navigation in 1855, with the completion of a channel 18 m wide and 3 m deep in the middle channel of the St. Clair Delta and the first navigation lock in the St. Marys Rapids.

Immediately after the opening of the upper Great Lakes to navigation, the rivers were modified to allow the passage of larger vessels. In 1857, a channel 35 m wide and 4 m deep was cut through the lower St. Clair River and in 1856 a channel 45 m wide and 5–6 m deep was opened in lower Lake George of the St. Marys River. A second series of dredging projects, begun on the St. Lawrence, St. Clair, and St. Marys rivers a decade later, allowed vessels with drafts of 4.5 m to enter Lake Ontario by 1875 and those with drafts of 6.0–6.5 m to operate in the upper Great Lakes by the mid-1890's. Today the navigation channels of the connecting rivers of the Great Lakes are maintained at a statutory depth of 8.2 m (Bryce 1982; Larson 1981).

Hydropower development on the connecting rivers also began during the 19th century with the construction of a hydropower canal to divert water around the St. Marys Rapids. Hydropower facilities, together with navigation locks on both sides of the river, now use a significant portion of the St. Marys River flow at Sault Ste. Marie. Excess flow is discharged through a 16-gate control structure upstream from a remnant of the original St. Marys Rapids. River flow was brought under complete control in 1921, when the International Joint Commission began setting the monthly discharge, through its International Lake Superior Board of Control (Koshinsky and Edwards 1983).

The large, dependable volume of water and substantial head differential of the Niagara River are also used by Canada and the United States for hydroelectric generation. Total capacities of the power plants are 2 350 $m^3 \cdot s^{-1}$ in Canada and 3 115 $m^3 \cdot s^{-1}$ in the United States. Each of the power plants withdraws water from the upper Niagara River and discharges it downstream from Niagara Falls.

The current International St. Lawrence River hydropower development program was completed in 1958 (Bryce 1982). The Moses–Saunders Dam, which created Lake St. Lawrence, has a head of 24.7 m and is the only site for hydroelectric power production on the river; however, two other dams — Long Sault and Iroquois — are used by the International St. Lawrence River Board of Control to regulate outflow from Lake Ontario. The Iroquois Dam is farthest upstream and is normally in a fully open position. The Long Sault Dam, upstream from the Moses–Saunders Dam, is used to control water level in the power pool of the Moses–Saunders Dam.

TABLE 1. Summary of flow, watershed, and mean water quality characteristics for the connecting rivers of the Great Lakes.[a].

Characteristic	River St. Marys	 St. Clair	 Detroit	 Niagara	 St. Lawrence
River length (km)	121	63	41	58	869
Drop in elevation (m)	6.7	1.5	1.0	99.3	74.0
Mean discharge ($m^3 \cdot s^{-1}$)					
Annual	2 100	5 097	5 210	5 692	6 739
Maximum	3 738	6 570	6 654	7 505	9 911
Minimum	1 161	3 002	3 171	3 285	4 361
Max/Min ratio	3.2	2.2	2.1	2.3	2.3
Watershed area (10^3 km^2)					
Lake(s) above	82	117	1	26	19
Drainage basin	128	252	18	59	64
Cumulative total	210	579	598	683	766
Water quality					
Conductance (μmhos$\cdot$cm^{-1})	105	208	256	274	329
Total phosphorus (ppb)	3.6	5.5	9.0	9.4	13.2
Total kjeldahl nitrogen (ppb)	99	188	180[b]	170	232
NO_3+NO_2 (ppb)	302	310	298	265	256
Si (ppm)	2.3	1.06	0.67	0.46	0.24
pH (range)	(7.9–8.3)	(7.7–8.7)	(7.0–8.6)	(7.3–8.5)	(8.2–8.7)
Chloride (ppm)	1.28	5.94	6.90	15.30	24.20
Dissolved oxygen (ppm)	11.2	11.2	9.3	—	12.2
Alkalinity (ppm)	41.6	80.0	81.2	97.5	92.4
Chlorophyll *a* (ppb)	0.83	2.10	3.40	1.10	3.19

[a] Data collected by R. Stevens, Canada Centre for Inland Waters (CCIW), Burlington, Ontario for the St. Marys River (1983), St. Clair River (1980), and St. Lawrence River (1985). Data for the Detroit River are mean values for 1967 to 1982 from the STORET data system (Herdendorf 1987) or those collected by M. Charlton, CCIW, Burlington, Ontario in 1985. Data for the Niagara River collected by D. Rathke, Center for Lake Erie Area Research, Columbus, Ohio in 1985.

[b] Average value from Vaughan and Harlow (1965).

Water Quality

Water quality in all of the Great Lakes connecting rivers is good (Table 1). Cold, well-oxygenated water is discharged from Lake Superior and flows throughout the St. Marys River. However, sediments are contaminated on the Canadian side at Sault Ste. Marie, Ontario, where an industrial complex discharges effluents directly or indirectly into the river (Hamdy et al. 1978). Pollutants identified from sediments in this reach of the river include cyanide, phenols, metals, sewage, and oil (Table 2). Sediments on the United States side of the river are largely uncontaminated, except for high levels of chromium adjacent to an abandoned leather tannery 5 km upstream from Sault Ste. Marie, Michigan.

Concentrations of toxic materials are also elevated in the sediments in several areas in the SCDRS. The major source of pollution in the St. Clair River is the Sarnia industrial complex on the Ontario side of the upper river. Lower pollutant values are reported in the delta section; however, sampling there has been limited. In Lake St. Clair, sediments from the mid-lake area have been found to be contaminated with polychlorinated biphenyls (PCBs), hexachlorobenzene (HCB), octachlorostyrene (OCS), cadmium, and mercury (Table 2). The major source of pollution in the Detroit River — particularly the lower river — is associated with the Detroit industrial complex along the Michigan shore. Pollutants identified from the Detroit River inclue PCBs, HCB, OCS, oil and grease, cyanide, phenols, chromium, mercury, and cadmium (Table 2). In addition, a total of 15 polynuclear aromatic hydrocarbons (PAH) have been found at concentrations as high as 39 ppm. The levels of certain pollutants declined after some of these data were collected in the 1970's. Mercury in surficial sediments declined substantially between 1970 and 1980 (Hamdy and Post 1985). In contrast, Mudroch (1985) concluded that metal concentrations in Detroit River sediments were significantly higher in 1983 than in 1969–73; however, Pugsley et al. (1985) could not determine whether sediment PCB levels have decreased or remained static in the SCDRS over the last 10 years. Changes in the distribution and amount of contaminants in sediments is clearly difficult to assess, partly because of sediment transport and scattered zones of deposition typical of riverine systems.

Water entering the Niagara River from eastern Lake Erie is also of relatively high quality (Table 1). Pollution of the river is primarily from an industrial complex along the New York shoreline and from tributaries (Strachan and Edwards 1984). High concentration of certain contaminants — including PCBs, total DDT, mirex, and mercury — have been identified in Niagara River sediments (Table 2).

Water quality of the St. Lawrence River reflects that of upstream Lake Ontario and is generally good (Table 1). As in the other connecting channels however, localized areas of sediment contamination exist (Table 2). Sediments near Ogdensburg Harbor and Chimney Bay were found to contain oil and grease, chromium, lead, nickel, and measurable

TABLE 2. Summary of pollutants and contaminants reported in sediments from selected reaches of Great Lakes connecting rivers. Numbers shown are ranges of concentrations in parts per million (mg•kg^{-1}), unless otherwise indicated.

Pollutant	River/Lake					
	St. Marys[a, c]	St. Clair River[b, c]	Lake St. Clair[b, c]	Detroit[b, c]	Niagara[c]	St. Lawrence[d]
PCB (ppb)	0–3 306[e]	0–10 000	0.50	0–3 800	27–2 700	—
HCB (ppb)	—[g]	—	36–99	0–360	1–250	—
OCS (ppb)	—	1–79	0–30	0–10	—	—
PAH	—	—	—	0–39	—	—
DDT (ppb)	—	—	—	15–185[f]	1–190	—
Cd	0.2–1.8[e]	.05–19	.02–3.33	0–27	0.40–0.88	<3
Cr	2.7–78[e]	6–15[e]	3–26[e]	4–330	7–170	0.3–46
Cu	1.8–110[e]	7–55[e]	1–30[e]	3–150[e]	4–110	1.0–7.0
Fe	3 900–450 000	3 400–29 000	5 783–9 747	5 200–70 000	—	1 300–2 180
Hg	0–0.31[e]	.01–58	1–3	0–8	.01–.96	0.1–1.6
Ni	1.8–44[e]	6–24	4–33[e]	6–130[e]	6–38	2.0–42
Pb	7–130[e]	2–42	5–30	5–960	4–200	1.0–111
Zn	9.4–1 100	28–310[e]	11–130[e]	21–5 300[e]	26–460	5–346
Cyanide	0.01–14	0–0.4[e]	0–0.8[e]	0.25–2.94	—	0.2–1.24
Phenols	3–13	0–10	0–2.8[e]	0–3	—	0.06–0.84
Mirex	—	—	—	—	4–640	—
Oil	44–19 000	250–600	0–637[e]	100–29 000	—	5 000–25 000

[a] Hamdy et al. (1978).
[b] Limno-Tech, Inc. (1985).
[c] Kauss (1983).
[d] Scrudato (1978).
[e] Bertram et al. (1987).
[f] Thornley and Hamdy (1984).
[g] A dash means no data were located.

quantities of mercury (Scrudato 1978); in addition, sediments contained zinc in Ogdensburg Harbor and copper at Chimney Bay. Blue Church Bay, on the Canadian side of the river, was heavily polluted with mercury. Measurable quantities of PCBs and mirex were found at all Ogdensburg area sites and some samples contained appreciable amounts of cyanide. However, cyanide concentrations were below the U.S. Environmental Protection Agency polluted classification criteria.

Biota

Phytoplankton

Species composition of net phytoplankton in the Lake Nicolet reach of the St. Marys River is dominated by diatoms. Nannoplankton is common in Lake Superior and would be expected to contribute to the plankton composition of the river; however, its presence and contribution to biomass have not been documented (e.g. Munawar and Munawar 1978). Organisms common in the St. Marys River in 1980-83 (Liston and McNabb 1986a) included six planktonic diatoms (*Asterionella formosa, Cyclotella comata, Fragilaria crotonensis, Melosira islandica, Stephanodiscus hantzchia*, and *Synedra ulna*), and one benthic diatom (*Achnanthes minutissima*). A mixture of planktonic and benthic forms was also observed in the plume of the St. Marys River in Lake Huron by Kreis et al. (1983). The mean chlorophyll *a* value in the Lake Nicolet reach during ice-free seasons was 0.66 mg dry weight (DW)•m^{-3} (range 0.40 to 1.22) — a value typical of oligotrophic waters (Wetzel 1975).

Net production of phytoplankton in the St. Marys River was determined by measuring the uptake of aqueous ^{14}C-sodium bicarbonate over time (Wetzel and Likens 1979) at one station in the upper portion of the Lake Nicolet reach and another in the lower portion. Measurements at each station were made 0.5 m below the surface, at mid-depth, and at the bottom. The volume of the Lake Nicolet reach was determined by depth-interval planimetry, and production was expressed as either the average net primary production over 1-m^2 of bottom, or in metric tons for the entire river reach per year (Table 3).

The phytoplankton community of the SCDRS is also dominated by diatoms. The most common forms found in Lake Huron by Vollenweider et al. (1974) — *Cyclotella, Tabellaria, Fragilaria, Stephanodiscus, Melosira*, and *Synedra* — would be expected in the St. Clair River due to the river's rapid flushing time. *Fragilaria* and *Tabellaria* are dominant in the Detroit River (Williams 1963), and are common in Lake St. Clair except in July and August when blue-green algae, particularly *Oscillatoria*, are more prevalent (Winner et al. 1970). *Microspora*, a filamentous green algae typically found in quiescent waters, was also common in the plankton of Lake St. Clair. High winds and currents may transport this alga from wetland areas into the lake.

Phytoplankton standing crop and production for the St. Clair River (Table 3) are based on those from Lake Huron (Glooschenko et al. 1973; Wollenweider et al. 1974). Average standing crop from May to November in Lake Huron was 1.7 mg chlorophyll *a*•m^{-3} and mean production rate was 3 mg C•m^{-3}•h^{-1}. These values were converted to ash free dry weight (AFDW) by applying the

TABLE 3. Mean standing crop (g AFDW$\cdot$m^{-2}), net production (g AFDW$\cdot$m$^{-2}\cdot$yr^{-1}) and system production (metric tons AFDW$\cdot$yr^{-1}) of primary producers and consumers, and allochthonous inputs to the St. Marys, St. Clair, Detroit, and St. Lawrence rivers and Lake St. Clair.

	Lake Nicolet St. Marys River			St. Clair River			Lake St. Clair			Detroit River			St. Lawrence River		
	Standing Crop	Net Production	System Production	Sanding Crop	Net Production	System Production	Standing Crop	Net Production	System Production	Standing Crop	Net Production	System Production	Standing Crop	Net Production	System Production
Surface area (ha)			3 958			5 813			111 400			13 760			65 600
Mean depth (m)			3.1			7.8			4.4			4.6			9.5
Photic depth (m)			3.1			7.8			2.5			2.5			7.5
Primary producers															
Phytoplankton	0.056	5	198	0.45	67	3 900	0.64	54	60 160	0.67	54	7 430	1.40	295	193 390
Periphyton	—	12[a]	36[a]	2.0	26	1 160	2.5	32	16 720	3.0	39	4 370	5.0	65	21 050
Macrophytes															
Submersed	—	35	735	131[b]	164	2 290	46[b]	58	13 780	139[b]	174	12 650	88.4[b]	110	20 710
Emergent	—	650	1 940	532[b]	665	22 620	532[b]	665	60 990	374[b]	468	4 030	650 [b]	715	23 160
Total			2 909			29 970			151 650			28 480			259 100
Primary consumers															
Zooplankton	0.06	1.03	41	0.56	10.1	590	0.44	7.9	8 800	0.46	8.3	1 140	1.51	27.2	17 830
Macrozoobenthos	8.6	15.5	456	1.0	7.4	440	1.1	6.8	7 600	0.75	5.4	640	7.47	13.4	8 780
Secondary consumers															
Fish	0.7	1.2	29	8.7	5.2	300	2.3	1.4	1 520	3.4	2.1	280	6.7	4.0	2 590
Allochthonous inputs															
Terrestrial			—			140			90			260			2 540
Dircet sewage			805			427			29			25 655			1 096

[a] Periphyton in emergent wetlands only.
[b] Seasonal maximum standing crop.
[c] Ash free dry weight.

following ratios: 17.05 mg C/mg chlorophyll *a* (Paerl et al. 1976) and 1.98 mg AFDW/mg C (Lind 1979). An average daylight period of 10 h and a 50 % reduction in C values to account for night respiration (Vollenweider 1969) were used to estimate annual production. Since productivity data represented only seven months, an annual estimate was obtained by using 50 % of these values for the remaining five months (Vollenweider et al. 1974). The standing crop estimate was assumed to be representative of a yearly average (based on Fig. 3 of Glooschenko et al. 1973). A mean depth of 7.8 m for the St. Clair River was used to convert volumetric units to areal estimates, and it was assumed that the entire water mass was photosynthetically productive. Daily production rates per square meter were summed over the two periods and multiplied by the area of the river (5 813 ha) to estimate total annual production. The average annual phytoplankton biomass in Lake St. Clair (4.3 mg chlorophyll *a*$\cdot$m^{-3}) was derived from a variety of sources (Leach 1972; Michigan Water Resources Commission 1975; Bricker et al. 1976). Inasmuch as production data for Lake St. Clair (Winner et al. 1970) were available for only the littoral area and might not be representative of the entire lake, an annual turnover rate (production to biomass ratio) of 150 was used, based on the Lake Huron data. A mean depth of 4.4 m (1 m greater than the low-water mean), a photic zone of 2.5 m, and a surface area of 111 400 ha were used to calculate standing crop and annual production. The Detroit river was assumed to have the same biomass, daily production, and photic zone as Lake St. Clair, a mean depth of 4.6 m, and an area of 13 760 ha.

In the St. LawrenceRiver, Mills and Forney (1982) identified a total of 104 taxa of algae during 1976–78. A more intensive long-term study of Lake Ontario yielded 360 species (Vollenweider et al. 1974). Seasonally, diatoms dominated winter and spring biomass (30–60 %) and cryptophytes made up 45–70 % of the summer algal biomass. Thirteen common genera were *Asterionella*, *Melosira*, *Cyclotella*, *Stephanodiscus*, *Fragilaria*, *Scenedesmus*, *Ankistrodesmus*, *Cryptomonas*, *Chromulina*, *Ochromonas*, *Chroococcus*, *Anabaena*, and *Aphanizomenon*. These genera were also common in the early 1930's (Burkholder and Tressler 1932). Green and blue-green algae were important contributors to biomass from late summer to early fall (60 %) and blue-green algae represented 30 % of the fall biomass. Phytoplankton biomass typically peaked at 2.0–2.5 g$\cdot$m^{-3} wet weight (ww) during spring after ice breakup, declined through the summer to values near 1.0 g$\cdot$m^{-3}, and sometimes increased slightly in fall. Winter biomass value ranged from 0.2 to 0.6 g$\cdot$m^{-3} ww (Mills et al. 1981). Chlorophyll *a* values averaged 4.3 mg$\cdot$m^{-3} (range 1 to 12) in the St. Lawrence River and 6 mg$\cdot$m^{-3} in surface waters of Lake Ontario near the St. Lawrence River (Glooschenko et al. 1972). Summer productivity measured by Mills and Forney (1982) in the river averaged 1 300 mg C$\cdot$m$^{-2}\cdot$d^{-1}, compared with annual estimates of 550 and 920 mg C$\cdot$m$^{-2}\cdot$d^{-1} in Lake Ontario near the headwaters (Glooschenko et al. 1974; Stadelmann et al. 1974). Phytoplankton standing crop was greatest in the headwaters and declined about 60 % between Cape Vincent and Lake St. Lawrence (Mills and Forney 1982).

Phytoplankton production in the St. Lawrence River (Table 3) was estimated in the same way as in the SCDRS. Average phytoplankton biomass (4.3 mg$\cdot$m^{-3} chlorophyll *a*) was converted to grams AFDW, then multiplied by mean depth (9.5 m) to arrive at a standing crop estimate of 1.38 g AFDW•m^{-2}. Primary production measured by Mills and Forney (1982) was representative of three summer months only. To account for the lower production during winter, we obtained a weighted annual average for each of the three river segments (Fig. 1) by assuming monthly production during other seasons to be 50 % of that in summer. Production within each segment was then calculated, a mean production estimate weighted by the area of river segment was derived, and this estimate was multiplied by the total area of the river (65 600 ha) to obtain production in the system.

Periphyton

Little information exists on the periphyton of the Great Lakes connecting rivers. The periphyton of emergent wetlands in the St. Marys River consists primarily of diatoms, the dominant taxon being *Diatoma* spp. The net primary production of periphyton on shoots of the dominant emergent macrophytes in the Lake Nicolet reach of the St. Marys River, *Scirpus acutus* and *Sparganium eurycarpum*, were made by applying the ^{14}C method used for phytoplankton. For each macrophyte species, sections of plant stems 9.5–9.8 cm long, with periphyton attached, were incubated in four light and four dark bottles spiked with ^{14}C-sodium bicarbonate. After incubation, the periphyton from 1 cm sections of the macrophyte stems were collected and the algal cells processed in the same way that phytoplankton was processed. Net periphyton productivity in these emergent wetlands ranged from 20 to 40 mg C•m^{-2} of plant surface per day and averaged 32 mg C•m^{-2} for the total growing season (Liston and McNabb 1986a). This value amounted to about 12 g AFDW net production per square meter during the ice-free portion of the year (Table 3).

Periphyton studies are unavailable for the SCDRS; however, a recent study in nearby western Lake Erie by Manny et al. (1985) provided some insight into what the community composition might be in the system. The diatoms *Gomphonema* and *Diatoma*, green algae (primarily *Ulothrix*), the blue-green alga *Oscillatoria*, and the red alga *Bangia* were common overwintering taxa. *Cladophora*, a filamentous green algae, dominates in summer (June–August).

Published estimates of periphyton standing crop derived from a variety of substrates range from 1 to 7 g AFDW•m^{-2} (Wetzel 1983). On the basis of these data, we assumed conservative mean annual estimates of 2.0, 2.5, and 3.0 g•m^{-2} on all colonized surfaces in the St. Clair River, Lake St. Clair, and Detroit River, respectively. Surface area of plant material (m^2) available for epiphyte colonization per m^2 of bottom was 1.22 for submersed macrophytes (Brown et al. 1988), and 0.75 for emergent macrophytes (B. Manny, National Fisheries Center–Great Lakes, unpubl. data). Epipelic and epilithic algae were assumed to develop in areas where plants were lacking, at depths of 0–3.6 m in the St. Clair River, and because light penetration was reduced, to 0–1.8 m in Lake St. Clair and the Detroit River (Hudson et al. 1986). An annual turnover ratio of 13 was taken from Wetzel (1975). The mathematical product of bottom surface area available, adjustments for macrophyte surface area, standing crop, and turnover ratio equaled annual production values for periphyton (Table 3).

Cursory studies of the St. Lawrence River periphyton community indicated that a variety of diatoms and green algae had colonized microscope slides retrieved after 30 d (Mills and Forney 1977). Standing crop averaged 6.8 g AFDW•m^{-2} at a deep station and 3.1 g AFDW•m^{-2} at a shallow station. *Cladophora* was the dominant epiphytic alga on aquatic macrophytes. Standing crop of *Cladophora* measured as dry weight (DW) increased from 0.25 g•m^{-2} in June to 22.5 g•m^{-2} in August (Mills and Forney 1977). Muenscher (1932) noted the presence of both *Cladophora* and *Rhizoclonium* in the St. Lawrence River during late August.

The littoral area available for production of periphyton in the international section was obtained from Patch and Busch (1986) for the United States side and doubled to approximate the area along both shores. We estimated that the 29 590 ha littoral area included 16 700 ha of submersed vegetation, 1 620 ha of emergent vegetation, 620 ha of forested wetlands, and 10 650 ha of unvegetated sediment. An average periphyton standing crop of 5.0 g AFDW•m^{-2} was assumed for all substrates and production estimates were calculated as they were for the SCDRS.

Macrophytes

The aquatic mcarophyte communities of the Great Lakes rivers have been relatively well described, although data gaps remain for some areas. In the St. Marys River, the species composition, standing crop, and production of submersed and emergent macrophytes were studied by Liston and McNabb (1986a). Species composition, distribution, and standing stock of submersed macrophytes were determined from samples collected by divers using SCUBA and with a Ponar grab. To obtain standing stock biomass estimates, divers swam transects from the navigation channel to shore, collecting 10–20 samples from each macrophyte bed encountered. These samples were then rinsed clean and dried to constant weight in an oven at 105°C and the dry weights were recorded to the nearest 0.01 g. Dried samples were then macerated and a 1-g subsample was combusted in a muffle furnace at 550°C to determine ash free dry weight. Productivity of submersed macrophytes was estimated by using the light and dark bottle techniques described by Wetzel and Likens (1979) on six dates from June 12 to October 19, 1983. This technique involved placing macrophyte shoots in light and dark bottles and incubating them at depths within the depth distribution of the species. After incubation, dissolved oxygen concentrations were determined, AFDW of the macrophyte tissue in bottles was measured, and net production or respiration was expressed as Δ mg 0_2•h^{-1}•g^{-1} ADFW of tissue (Liston and McNabb 1986b). Production was later converted from units of oxygen to mass from photosynthetic quotients of 1 to 3.

Three species of macrophytes dominated the submersed flora in the St. Marys River (Liston and McNabb 1986a): The quillwort *Isoetes riparia* occurred in monotypic stands between depths of 2.0 and 3.5 m, and the charophytes *Nitella flexilis* and *Chara globularis* were in monotypic or mixed stands. Among charophytes, *Nitella flexilis* grew in the deepest water and formed the lower boundary of the vegetated zone. Depth of the lower boundary was about 14 m at the head of the river and 3-m in downstream reaches. During studies in 1979–83, maximum biomass was in submersed macrophyte meadows in September, where it averaged 35 g (range 10–70 g) AFDW•m^{-2}.

Distribution and coverage of emergent macrophytes in the Lake Nicolet reach of the St. Marys River were mapped by aerial photography and ground surveys in 1981–83 (Liston and McNabb 1986a). Standing stock biomass of both shoots and rootstocks was determined during winter and throughout the growing season. Methods used to determine AFDW were similar to those described for submersed macrophytes, except that live and dead roots were distinguished for emergent machrophytes. To estimate production of the two dominant emergent macrophytes, *Scirpus acutus* and *Sparganium eurycarpum*, gas exchange was measured on sections of stems or leaves. From these data, calculated net carbon fixed per square meter was calculated and transformed to production as organic mass.

Emergent wetlands of the St. Marys River are dominated by three species of macrophytes (in decreasing order of abundance): *Scirpus acutus*, *Sparganium eurycarpum*, and *Eleocharis smallii* (Liston and McNabb 1986a). Relatively small stands of *Phragmites australis*, *Scirpus americanus*, and *Typha latifolia* are also present. Rootstocks of these plants occur primarily in the upper 20 cm of clay sediments that cover extensive shallow littoral margins of the river. The annual biomass of shoots germinating from emergent rootstocks peaks in September. Maximum annual biomass (AFDW) in stands of emergent vegetation averages 650 g•m^{-2} for shoots and 990 g•m^{-2} for rootstocks.

In the St. Marys River, net productivity of plant communities in the Lake Nicolet reach (Table 3) reflected productivity for the growing season of May through October. In converting this value to an annual basis we assumed that productivity is nil during the very low temperature and light conditions of winter. Empirical observations showed this assumption to be more valid for emergent and submersed wetlands than for phytoplankton.

At least 21 taxa of submersed macrophytes occur in the SCDRS (Hudson et al. 1986; Schloesser and Manny 1986); the most common, in decreasing order of occurrence, follow: *Chara* spp., *Vallisneria americana*, *Najas flexilis*, *Myriophyllum spicatum*, *Elodea canadensis*, *Potamogeton richardsonii*, narrow-leaf forms of *Potamogeton* spp., and *Heteranthera dubia*. *Chara* was most common in the St. Clair River and Anchor Bay and *Vallisneria* was most common in Lake St. Clair proper and the Detroit River. Macrophyte stands were typically composed of two to three species (maximum 11); *Chara* was the only taxon consistently occurring in monotypic stands. The lower boundary of the vegetated zone has not been adequately documented, but most stands were at depths of less than 3.7 m. This depth range (0–3.7 m) covers about 16, 628, and 99 km^2 in the St. Clair River, Lake St. Clair, and Detroit River, respectively. Plant cover above this depth varied from non-existent at sites adjacent to bulkheaded areas along the Detroit River, to 92 % in Anchor Bay of Lake St. Clair. Average plant coverage on or inside the 3.7 m depth contour was 88, 35, and 72 % in the St. Clair River, Lake St. Clair, and the Detroit River, respectively. Estimates of average biomass (AFDW) range from 39 g•m^{-2} at 1.8–3.7 m depth of Lake St. Clair to 142 g•m^{-2} in the 0–1.8 m zone of the lower Detroit River.

Production is usually assumed to equal maximum standing crop; however, production is rarely sampled at its peak, and grazing, physical damage, and other mortality imply a ratio greater than 1. We arbitrarily chose a production to maximum biomass ratio of 1.25, which we assumed to be conservative (Rich et al. 1971). The product of the surface area within the 0–3.7 m contour, percent coverage, the constant 1.25, and maximum standing crop as AFDW equaled total production of submersed macrophytes in the SCDRS (Table 3).

Emergent macrophytes in the SCDRS were studied by Hudson et al. (1986) at Stoney Island in the Detroit River and by B. Manny (National Fisheries Center–Great Lakes, Ann Arbor, MI, unpubl. data) in Anchor Bay, Lake St. Clair. Large-scale mapping of wetland community types has also been completed for the system (Jaworski and Raphael 1976; Lyon 1979; Herdendorf et al. 1981; Raphael and Jaworski 1982; McCullough 1985). More than 95 % of the emergent macrophytes beds in both rivers occur in the lower river sections. At Stony Island, *Typha angustifolia*, *Sparganium eurycarpum*, *Scirpus fluviatilis*, and *S. americanus* contributed most to the biomass of emergent macrophytes (Hudson et al. 1986). In Anchor Bay, *Typha latifolia*, *T. angustifolia*, *Scirpus validus*, *Phragmites communis*, and *Eleocharis quadrangulata* were the predominant taxa contributing to above- and below-ground biomass. The total area of undiked emergent wetlands in the St. Clair River, Lake St. Clair, and the Detroit River were estimated to be 3 380, 9 170, and 860 ha, respectively. Maximum standing crop (AFDW) of emergent macrophytes was set at 532 g•m^{-2} in the St. Clair River and Lake St. Clair and 374 g•m^{-2} in the Detroit river. Production was estimated by multiplying maximum standing crop by 1.25 to account for grazing, physical loss, and other mortality.

In the St. Lawrence River, seven of 19 recorded species dominated the submersed flora of littoral areas. These seven species either represented high proportions of the biomass or had a high relative importance within stands (Ruta 1981). Submersed macrophyte communities in less than 3-m of water were dominated by *Myriophyllum exalbescens*, *Vallisneria americana*, *Potamogeton zosteriformis*, *Ceratophyllum demersum*, and *Elodea canadensis*. The community at depths of 3.0–7.5 m was dominated by *Nitellopsis obtusa*, *C. demersum*, *Elodea* spp., *Vallisneria*, and *Potamogeton pectinatus*. Except for the recently introduced *N. obtusa* (Geis et al. 1981), and the increase in abundance of *P. zosteriformis*, this deepwater community was similar to that reported from earlier studies by Muenscher (1931, 1932). Biomass of submersed macrophytes over all plots studied by Ruta (1981) averaged 96 g (maximum, 360 g) AFDW•m^{-2}. Macrophyte stands were common in the upper section of the St. Lawrence River, where water current was moderate and numerous islands and shoals prevail and in the lower section of the river near Waddington, New York (Patch and Busch 1986). The amount of littoral area with submersed macrophytes (27 350 ha) was obtained from maps published by Patch and Busch (1986). Percent coverage was estimated from their qualitative descriptions of macrophyte beds to be 80, 50 and 30 % in the upper, middle, and lower sections, respectively. Maximum biomass (AFDW) for the first two sections, 112 and 72 g•m^{-2}, was derived from Ruta (1981) and the value of 50 g•m^{-2} for the lower section was approximated from qualitative descriptions by Patch and Busch (1986). Production estimates were calculated as they were for the SCDRS.

Geis and Kee (1977) reported that emergent wetlands of the St. Lawrence River were dominated by eight species of macrophytes: *Typha glauca*, *Carex stricta*, *Calamagrostis canadensis*, *Phalaris arundinacea*, *Sparganium eurycarpum*, *Peltandra virginica*, *Sagittaria latifolia*, and *S. rigida*. These authors identified four community types, ranging from cattails to grass and sedge meadows. Patch and Busch (1986) measured 1 620 ha of emergent wetlands for the United States portion of the international section of the river. Maximum biomass (DW) of emergent macrophytes ranged from 736 $g \cdot m^{-2}$ in healthy streamside stands to 567 $g \cdot m^{-2}$ in stands influenced by high water (Gilman 1976). This area was doubled to include the Canadian shoreline, and an average of the two biomass estimates was converted to AFDW and multiplied by 1.25 to arrive at an estimate of production for emergent macrophytes.

Zooplankton

Although a considerable body of literature has been amassed for the zooplankton of the Great Lakes, little information is directly available for connecting rivers. The zooplankton in Whitefish Bay, immediately above the St. Marys River, consisted of 30 species (Selgeby 1975). Seasonally, the winter zooplankton consisted primarily of adult stages of *Diaptomus sicilis*, *D. ashlandi*, and *Limnocalanus macrurus* and copepodids of *Cyclops bicuspidatus thomasi*. *Mysis relicta* also contributed substantially to the biomass of the winter zooplankton. During summer, immature Calanoida, adult *C. b. thomasi*, and Cladocera predominated in the open water. The summer zooplankton of emergent wetlands in the St. Marys River was dominated by Cladocera, with many small benthic or epiphytic species (Duffy 1985).

The standing stock of zooplankton biomass measured several kilometers upstream from the Lake Nicolet reach averaged 18.6 mg $AFDW \cdot m^{-3}$ from November 1971 to November 1972 (Selgeby 1975). Since flushing rate of the Lake Nicolet reach was less than 24 h, we assumed that standing stock immediately upstream was representative of that in the lake. We calculated zooplankton production for the open-water portion of the Lake Nicolet reach by multiplying annual average standing stock by a turnover ratio of 18 — a value representative of mesotrophic lakes (Wetzel 1983) — and then extrapolating this to the volume of the lake. Estimates of zooplankton production in emergent wetlands of the Lake Nicolet reach were measured in summer 1983 by Duffy (1985), who used the instantaneous growth method of Waters (1977). These data were also extrapolated to the volume of water in emergent wetlands bordering the river reach. Data presented in Table 3 are average production per unit area of both habitats, and total production of the river reach.

Comprehensive studies of zooplankton in the SCDRS have been limited to Lake St. Clair (Winner et al. 1970; Leach 1973; Bricker et al. 1976), the St. Clair River (Texas Instruments 1975), and Lake Huron (Watson and Carpenter 1974). *Bosmina longirostris* and several species of *Cyclops* and *Diaptomus* dominated in the St. Clair River but were replaced by *C. vernalis* and *D. ashlandi* in Lake St. Clair. This switch, plus increases in abundance of zooplankton in Lake St. Clair along a transect from northwest to southeast reflected a pattern of increased eutrophication of the lake. A total of 14 taxa of planktonic copepods and 18 of cladocerans have been reported in the SCDRS. The most common protozoan was *Difflugia*, and the most common rotifers were *Conochilus*, *Keratella*, *Polyarthra*, *Synchaeta*, and *Brachionus*. Zooplankton density peaked between June and September. Average zooplankton standing crop (AFDW) in Lake Huron from May to December was 0.051 $g \cdot m^{-3}$ (Watson and Carpenter 1974). The incorporation of winter declines similar to that in the St. Lawrence River (Mills et al. 1981) yielded an annual mean of 0.036 $g \cdot m^{-3}$ for the SCDRS. These estimates were based on tows from a depth of 50 m, and since zooplankton tends to be in the upper layer (Wells 1960), this value was doubled and multiplied by mean depth to arrive at a standing crop of 0.56 $g \cdot m^{-2}$. Inasmuch as standing crop estimates for Lake St. Clair are not available, we arbitrarily used a value of 0.100 $g \cdot m^{-3}$, based on standing crops for mesotrophic lakes (Wetzel 1975). This value was also used for the Detroit River. The annual turnover ratio of 18 that was used to estimate production represented an average of several turnover times given for oligotrophic and mesotrophic waters (Wetzel 1975).

The zooplankton in the upper St. Lawrence River is very stable, reflecting the influence of Lake Ontario, and declines substantially (80–90 %) down river (Mills and Forney 1982). The community contains at least 29 species of copepods, cladocerans, and rotifers. *Cyclops bicuspidatus* and *Diaptomus minutus* are and have been the most common copepods and *Bosmina longirostris* the dominant cladoceran, in both summer and winter (Burkholder and Tressler 1932). Common rotifers include *Asplanchna*, *Conochilus*, *Kellicottia*, *Keratella*, *Notholca*, and *Polyarthra*. These taxa are also dominant in Lake Ontario (Watson and Carpenter 1974). Zooplankton biomass ranged from 10 to 500 mg $AFDW \cdot m^{-2}$ during the winter months (Mills et al. 1981) and from 27 to 7 200 mg $AFDW \cdot m^{-2}$ during the summer month (Mills and Forney 1982). Biomass peaked in late July to early August but estimates between years varied by up to a factor of 3. Calculation of zooplankton production for the river was fairly straightforward. Summer offshore and inshore biomass data for each section were averaged with winter data to obtain a yearly mean. These means were weighted by a profundal to littoral zone ratio (43, 31, 56 % littoral area in the upper, lower and middle section) and percent total area (62, 11, 27 %) in each of the three river sections to obtain a riverwide average of 1.51 g $AFDW \cdot m^{-2}$. Multiplication by a turnover ratio of 18 and the total area of the river provided the net and system production estimates in Table 3.

Benthic Macroinvertebrates

The Great Lakes connecting rivers support a diverse and abundant benthic macroinvertebrate fauna: more than 300 taxa were identified in both the St. Marys River (Duffy et al. 1987) and the SCDRS (Hudson et al. 1986). In the St. Marys River, high-quality water entering the river from Lake Superior and the varied habitats present (which include rock rapids, emergent wetlands, submersed vegetation, and numerous sediment types) contribute to the diversity of macroinvertebrates that have been observed (Hiltunen 1978; Liston et al. 1983; Duffy et al. 1987). Analysis of benthic macroinvertebrates in the St. Marys River by habitat during a 2-yr study by Duffy et al. (1987) revealed 118 taxa within the emergent wetlands; of these, 41 were unique to this habitat — including species of Odonata, Lepidoptera, Coleoptera and non-chironomid Diptera. Predators and herbivores were both well represented in emergent wetlands. Of 120 taxa identified at offshore sites, 42 (including mollusks, Trichoptera, and Chironomidae) proved to be unique to this habitat. Omnivores were the most common functional group at offshore sites. Within the navigation channel, only 37 taxa were collected, none of which were restricted to the channel habitat.

Numerically, chironomid larvae have dominated macroinvertebrate samples from the St. Marys River, composing 7.8–98.4 % (usually 40–60 %) of the benthos at individual stations. Chironomidae tend to be more abundant at intermediate depths where water currents are moderate and the substrate is coarse. Oligochaeta are also abundant in the river system and typically compose the second most numerous taxonomic group. Together, oligochaetes and chironomids generally made up 60–90 % of the benthos at a site. Other organisms, which were common and contributed more to the standing crop by virtue of their larger size, included the burrowing mayflies *Hexagenia limbata* and *Ephemera simulans*, the caddisfly *Polycentropus* sp., and a variety of mollusks, amphipods, and isopods. Crayfish are abundant in portions of the river, but little quantitative information exists for these animals.

Except in the navigation channel, the abundance of benthic organisms is generally higher throughout the river than in either northern Lake Huron or Whitefish Bay (Liston et al. 1981; Duffy et al. 1987). Estimates of total abundance ranged from 21 to 64 278•m^{-2} in 552 samples collected in 1982 and 1983 (Duffy et al. 1987). In the upper river, the west or lee side supports larger numbers of benthos than does the windward side. In the lower river, however, abundance appears to be distributed more evenly across the river in spring. In fall, emergent wetlands support high numbers of benthos, whereas offshore densities are lower and more uniform. Numbers are consistently lower in the navigation channel than elsewhere in the river.

Production of benthic invertebrates in the Lake Nicolet reach of the St. Marys River was measured in emergent wetlands and offshore habitats in 1981 and in the rapids at the lower end of the reach in 1983. We used the average cohort method to calculate production for common taxa in the wetlands or offshore habitat, and the instantaneous growth method of Waters (1977) to calculate the production of common taxa in the rapids habitat. We used turnover ratios to estimate production of uncommon taxa from all habitats. The area of each habitat in the Lake Nicolet reach was determined from planimetry of maps and annual production per unit area, extrapolated to total production for the reach (Table 3).

Annual production in dry weight (DW), estimated for 38 common benthic macroinvertebrate taxa of the St. Marys River, ranged from 14.5 to 24.7 g DW•m^{-2} (Table 4). Production in emergent wetlands was 6–41 % greater than in deeper water and about equal to production in the rapids (i.e. 20.0–24.7 g DW•m^{-2}•yr^{-1}). In emergent wetland communities, 11 taxa, as well as miscellaneous chironomids and oligochaetes, each contributed 5 % or more to the total annual production. In soft-bottom communities offshore, *Hexagenia limbata* and sphaeriid clams (collectors) contributed more than 50 % of the annual production in Lake George, whereas chironomids, *Hyalella azteca*, and oligochaetes (shredders and collectors) were most important to annual production in Lake Nicolet. In the Neebish Island Rapids, production has been calculated only for the most abundant organisms or those obviously contributing to production (e.g., crayfish). However, these data illustrate the potential for rapids to contribute to production in the river system.

Macroinvertebrates have been studied in all sections of the SCDRS (Ontario Ministry of the Environment 1979; Hiltunen 1980; Hiltunen and Manny 1982; Thornley and Hamdy 1984; Thornley 1985; Hudson et al. 1986). The most significant taxa, on a biomass basis, are the Oligochaeta, Chironomidae, Gastropoda, Ephemeroptera, Trichoptera, and Amphipoda. *Hydra* is abundant but contributes little to biomass. Oligochaetes are most common in the lower Detroit River, where tubificid species predominate. Chironomids are abundant throughout the system; the most common taxa are *Cricotopus, Parachironomus, Parakiefferiella, Rheotanytarsus*, and *Stictochironomus*. Common snail taxa are *Amnicola* and *Elimia*. *Hexagenia*, the most common mayfly, is more dense in Lake St. Clair and the lower St. Clair River. *Cheumatopsyche, Hydropsyche*, and *Oecetis* are dominant trichopteran taxa and *Hyalella* is the most common amphipod. Species richness within these taxa is greatest in Chironomidae (127), Trichoptera (49), and Oligochaeta (25). Freshwater mussels are represented by 24 known species (Freitag 1984), but like crayfish and salamanders they have not been adequately sampled.

Macroinvertebrate standing crops in the SCDRS were taken from Hudson et al. (1986). We calculated total biomass weighted by areas associated with depth contours of 0–1.8, 1.8–3.6, and >3.6 m in the two rivers. Data on standing crop for Lake St. Clair were taken from mid-lake samples. To estimate production, we used turnover ratios published by Waters (1977) for the 10 dominant taxa in each section of the system. A weighted turnover ratio for each

TABLE 4. Estimated total benthic invertebrate production of the St. Marys River (as mg•m^{-2}•yr^{-1}) in the littoral, offshore and rapids areas of Lakes Nicolet and George.[a]

	Locality and Total Production	
Habitat	Lake Nicolet	Lake George
Littoral	24 682	20 020
Offshore	14 464	19 846
Rapids	23 683	—

[a] Source: Duffy et al. (1987).

section was derived by using relative biomass of each taxon as the weighting factor. The relative biomass of each taxon in a section was obtained by multiplying numerical abundance by average individual biomass. Community turnover ratios ranged from six to eight, depending on the relative abundance of fast-growing chironomids, oligochaetes, nematodes, and polychaetes or slowing growing amphipods, mollusks, and mayflies.

Macroinvertebrate diversity in the international section of the St. Lawrence River is probably also high, but cannot be determined, since taxonomic treatment has rarely been below the family level (Mills et al. 1978; Patch and Busch 1986). Numerically, chironomids, oligochaetes, amphipods, hydra, and gastropods dominate. Amphipods were particularly abundant on aquatic macrophytes. The large rocks and rubble that predominated in the substrate — particularly in the upper river — made quantitative sampling difficult. Patch and Busch (1986), who sampled rocky areas extensively with a pump, found that sphaeriid clams and gastropods were abundant, but the attachment of a debris screen excluded larger mollusks. In finer sediments, densities averaged $141 \cdot m^{-2}$ for pelecypods and $5\ 000 \cdot m^{-2}$ for gastropods (Mills et al. 1978). Molluscan taxa in the river were *Elliptio, Lampsilis, Bithynia tentaculata, Goniobasis, Valvata*, and *Physa* (Magnin and Stanczykowska 1971; Patch and Busch 1986). In the Ogdensburg, New York, area, Mills et al. (1981) found large numbers of oligochaetes ($20\ 000 \cdot m^{-2}$), chironomids ($23\ 000 \cdot m^{-2}$), and nematodes ($2\ 000 \cdot m^{-2}$) in sediments associated with chemical and sewage effluents.

The distribution of large mollusks (having high biomass) in habitats within different sections of the river also presented problems in estimating the production of benthic invertebrates in the St. Lawrence River. Standing stock biomasses of pelecypods and gastropods as high as 1 100 g $AFDW \cdot m^{-2}$ and 34 g $AFDW \cdot m^{-2}$, respectively, have been recorded in the river. However, total standing stock biomass, excluding mollusks, averaged only 1.3 g $AFDW \cdot m^{-2}$ within depth contours of 1 to 15 m (Mills et al. 1978). Since Patch and Busch (1986) used both a Ponar grab and a pump to sample the river, their sampling probably represented all of the benthic habitats present. Of their samples in the Thousand Island Area (upper section), 20% were in fine sediments and could include mollusks — which Mills et al. (1978) estimated to weigh 111.7 g $AFDW \cdot m^{-2}$. Of the samples collected by Patch and Busch (1986), 80% were in rocky areas and AFDW averaged 2.5 $g \cdot m^{-2}$. These estimates were weighted by the percent coverage of each sediment size present in the littoral area of the upper section. Since profundal estimates have not been made, we used a biomass of 0.5 g $AFDW \cdot m^{-2}$, which is similar to the channel estimates made in the SCDRS. These estimates were then weighted by the profundal-littoral ratio. Turnover rates of 1.5 for gastropods and 0.2 for pelecypods were taken from Waters (1977) and weighted by their relative biomass contributions, to arrive at a turnover ratio of 0.9 for mollusks. For benthic invertebrates other than mollusks, a turnover ratio of 8 was used. This procedure was also used in the middle section. Similar taxonomic composition and standing stock biomass (0.5 g $AFDW \cdot m^{-2}$) have been reported for the lower section of the river (Mills et al. 1978; Patch and Busch 1986). The standing crop and production estimates for each section were then weighted by the area of each section to arrive at an average for the river (Table 3).

Fish

Species richness in the fish communities of the connecting channels is high throughout the system, with 75, 90, 60 and 99 species recorded in the St. Marys, St. Clair, Detroit, and St. Lawrence rivers, respectively (Greeley and Greene 1931; Haas et al. 1985; Patch and Busch 1986; Duffy et al. 1987).

In a 5-yr study of the Lake Nicolet reach of the St. Marys River, 42 fish species of all life stages were collected (Liston et al. 1981, 1983; Liston and McNabb 1986b). The fish were collected with a variety of gears, including larval fish nets, large and small trap nets, bottom trawls, and bottom gill nets (Liston and McNabb 1986b). Areas sampled included the channel, the shallow open waters east of the channel to the edge of emergent macrophytes, and the emergent plant beds.

Seventeen taxa of larva fish were identified in Lake Nicolet. Densities were usually greatest in stands of emergent macrophytes. Densities of 9 taxa in 1982 and 13 taxa in 1983 peaked in the beds of emergent vegetation. Habitats in open waters near the edge of emergent plants supported intermediate larval densities, in general, and the navigation channel area contained the fewest larvae. This general distribution of larvae held along many reaches of the St. Marys River (Liston and McNabb 1986a). Larval rainbow smelt (*Osmerus mordax*) were an exception, the greatest densities being associated with the channel.

Relative abundance of fish species in the St. Marys River from two areas and three different habitats, based on collection with four types of gear, is given in Table 5 (common and scientific names of species collected are shown in Table 6). The number of species collected by each gear was similar, ranging from 17 in large trapnets to 25 in gill nets, but relative abundance varied greatly. This variation reflects partly the type of gear used but also habitat preference. Young-of-the-year sunfishes were by far the most numerous taxa in the emergent wetlands. However, in terms of biomass, white sucker dominated, followed by brown bullhead. Large adults of these two species were common, whereas most other species were represented by either small species or small juveniles. Small forage fishes or small fish of other species also dominated the catch in the submergent wetlands. Number and weights were more equitable in the deeper offshore areas.

Fish standing crop estimates could be extrapolated from offshore otter trawl sampling. An average of 0.9 kg of fish biomass was collected per $1\ 000 \cdot m^2$ of substrate. This average converts to a more conventional unit of 9 $kg \cdot ha^{-1}$ wet weight or 81 mg $AFDW \cdot m^{-2}$. This value is lower than the standing crop estimates for the entire river found in Table 3, and reflects the selectivity of the otter trawl toward smaller specimens.

A comprehensive description of the fish spawning and nursery areas of the SCDRS revealed spawning habitat for resident fish and migratory species from lakes Huron and Erie (Goodyear et al. 1982); 28 species are known to spawn in the St. Clair River and 32 in the Detroit River.

Tow net catches of fish larvae in the SCDRS in 1977–78 and 1983–83 (Hatcher and Nester 1983; Muth et al. 1986)

TABLE 5. Species composition and rank of dominant fish species in two areas and three vegetation types, collected by four types of gear in the Lake Nicolet reach of the St. Marys River, 1981–83[a]. (See Table 6 or text for most of the scientific names.)

Nearshore		Offshore	
		Non-Vegetated	
Emergent (small trap net)[f]	Submersed (otter trawl)[g]	(gill net)[h]	(large trap net)[i]
Sun fishes	Trout perch[b]	Lake herring	White sucker
Brown bullhead	Mimic shiner	White sucker	Rock bass
Yellow perch	Mottled sculpin	Yellow perch	Walleye
Mimic shiner[c]	Logperch	Northern pike	Yellow perch
White sucker	Spottail shiner	Walleye	Brown bullhead
Rock bass	Johnny darter[c]	Rock bass	Redhorse
	Rock bass		Smallmouth bass
	White sucker		Northern pike
	Yellow perch		
	Ninespine stickleback[b]		

[a] Source: Liston and McNabb 1986a.

[b] *Percopsis omiscomaycus*.

[c] *Etheostoma nigrum*.

[d] *Pungitius pungitius*.

[c] *Notropis volucellus*.

[f] 15.2 × 1.0 m lead; 2.6 × 1.0 m wings; 1 m^2 pot; 6.35 mm bar mesh.

[g] Shell 38 mm bar mesh; cod end liner 3 mm bar mesh; 4.4 m head rope.

[h] Seven continuous panels 15.2 m × 1.8 m with stretch mesh of 25, 51, 63, 76, 102, 114, 178 mm, respectively.

[i] 91.4 × 1.5 m lead, 1.2 × 1.8 × 3.1 m pot, 5.17 stretch mesh.

showed that the St. Clair River is a nursery for at least 26 species and the Detroit River is a nursery for at least 25. Average density and relative abundance data indicated that the alewife, rainbow smelt, log perch (*Percina caprodes*), emerald shiner (*Notropis atherinoides*), and gizzard shad dominated the catches of larvae from the St. Clair River, and that the alewife, rainbow smelt, and gizzard shad dominated the catches from the Detroit River. The average density of all larvae combined was 206 and 275 per 1 000 m^3 for the St. Clair and Detroit rivers, respectively, during the study period (Muth et al. 1986).

Populations of juvenile and adult fishes in Michigan waters of the SCDRS were studied from March 1983 to April 1985 by Haas et al. (1985). Their study was conducted in three segments: a trap net survey a tagging study, and an angler creel survey. The trap net survey provided relative abundance data and catch per net lift, and was a source of fish for tagging. The traps used were nearly identical to those used by Liston and McNabb (1986b) in the St. Marys River study. Analysis of tag-recapture data provided information on species dispersal and an estimate of stock size. The creel analysis provided estimates of angler catch and catch per unit of effort (CPUE), by species.

A total of 57 579 fish, representing 57 species were netted (Table 6). The catch can be described as a mixture of riverine and lake species. As judged by the trap net CPUE, habitat associations were made for certain species. Longnose gar, northern pike, common carp, and yellow perch seemed to prefer the lower portion of both rivers, where macrophytes predominated. Freshwater drum and channel catfish seemed to prefer the lake and lower portions of both rivers. White perch, white bass, and goldfish were dominant in the lower portion of the Detroit River and probably reflected the influence of Lake Erie, where these fish are abundant. Alewife declined steadily from the upper St. Clair River downstream — probably reflecting the influence of Lake Huron, where this species is abundant. The overall CPUE was nearly identical for the upper river sections (i.e., 14.9 and 14.6) and the lower sections (32.7 and 30.3); CPUE for Lake St. Clair was intermediate. The influence of the extensive macrophytes in the lower sections of the two rivers cannot be ignored as a major factor in this difference.

A total of 63 species of fish that could possibly spawn in the international section of the St. Lawrence River were identified by Patch and Busch (1986), who collected fish eggs from April to July (June was the dominant egg deposition month). They identified rainbow smelt, spottail shiners (*Notropis hudsonius*), greater redhorse (*Moxostoma valenciennsei*), brown bullhead, smallmouth bass, and walleye as potential spawners in much of the river, whereas muskellunge (*Esox masquinongy*), northern pike, largemouth bass, yellow perch, and mottled sculpin (*Cottus bairdi*) were limited to certain areas. A larger variety of species spawned in the Lake St. Lawrence section than in upriver sections. Larval sculpin were the most common fish collected with a pump. In samples of larval fish made with a plankton net in July–August 1976 in the upper section of the river, alewife made up 94 % of the catch (Werner 1977). Other species, in decreasing order of abundance, were pumpkinseed, yellow perch, bluegill, largemouth bass, and spottail shiner. Marean (1976) found the eggs or larvae of 14 species — particularly of largemouth bass — in a wetland along the St. Lawrence River. Sampling in April and May by NALCO Environmental Sciences (1978) yielded larvae of four species, among which yellow perch were abundant at inshore locations and rainbow smelt, alewife, and burbot (*Lota lota*) were abundant in channel locations.

The status of 99 species of fish collected in the St. Lawrence River and 21 species found nearby that may stray into the river, was summarized by Eckert and Hanlon (1977). Werner and Ford (1972) provided specific distribu-

TABLE 6. Catch per unit effort for the major species collected in St. Clair–Detroit River system during a trap net study, March 1983 through April 1985 (from Haas et al. 1985).

Species	Upper St. Clair River	Lower St. Clair River	Lake St. Clair	Upper Detroit River	Lower Detroit River
Longnose gar, *Lepisosteus osseus*	0.01	0.07	0.02	0.01	0.15
Bowfin, *Amia calva*	—	0.18	0.02	—	0.03
Alewife, *Alosa pseudoharengus*	2.20	0.65	0.12	0.02	0.09
Gizzard shad, *Dorosoma cepedianum*	0.31	0.23	0.10	0.27	0.30
Rainbow smelt, *Osmerus mordax*	1.11	0.56	—	0.01	—
Northern pike, *Esox lucius*	0.09	0.51	0.06	0.16	0.27
Brown bullhead, *Ictalurus nebulosus*	—	0.29	—	0.84	1.06
Channel catfish, *Ictalurus punctatus*	0.17	0.52	1.24	0.18	0.52
Stonecat, *Noturus flavus*	0.02	0.04	0.47	0.38	0.25
White perch, *Morone americana*	0.03	0.38	0.73	0.61	7.00
White bass, *Morone chrysops*	0.18	0.23	0.38	0.13	0.66
Freshwater drum, *Aplodinotus grunniens*	0.17	0.74	0.96	0.29	0.43
Goldfish, *Carassius auratus*	—	—	—	0.02	0.17
Common carp, *Cyprinus carpio*	0.19	1.41	0.16	0.37	2.10
Quillback, *Carpiodes cyprinus*	—	0.12	0.27	0.06	0.31
White sucker, *Catostomus commersoni*	1.37	0.90	0.29	0.19	0.46
Northern hog sucker, *Hypentelium nigricans*	0.06	0.02	—	—	—
Redhorse spp., *Moxostoma*[a]	0.67	0.66	1.70	0.30	0.59
Rock bass, *Ambloplites rupestris*	2.81	10.07	6.18	4.83	5.78
Pumpkinseed, *Lepomis gibbosus*	0.12	2.90	0.04	0.34	0.22
Bluegill, *Lepomis macrochirus*	0.03	0.12	0.02	0.53	0.03
Smallmouth bass, *Micropterus dolomieui*	0.45	0.47	3.04	1.11	0.41
Largemouth bass, *Micropterus salmoides*	0.01	0.16	—	0.04	0.02
Black crappie, *Pomoxis nigromaculatus*	0.03	0.92	0.08	0.28	0.41
Yellow perch, *Perca flavescens*	2.82	7.93	2.89	3.34	6.42
Walleye, *Stizostedion vitreum*	1.89	2.38	4.40	0.88	2.34
Others	0.12	0.20	0.15	0.15	0.26
Total	14.87	32.68	22.34	14.58	30.26
Total Units of Effort[b]	642	353	550	342	617

[a] Mostly shorthead redhorse (*M. macrolepidotum*), but including silver (*M. anisurum*), golden (*M. erythrurum*) and river redhorses (*M. carinatum*).

[b] A unit of effort is one trap-net set for 24h (see Table 5 large trap-net for size).

tions of important sport and commercial species and identified 11 warmwater species that are important contributors to the economy of the region: smallmouth bass, northern pike, yellow perch, brown bullhead, muskellunge, rock bass, white perch, white bass, pumpkinseed, largemouth bass, and walleye. The occurrence and relative abundance of these species, excluding white bass and including lake sturgeon and bluegill, in the St. Lawrence River was evaluated for a 50-yr period (Table 7). As judged by catches in a variety of sampling gears, yellow perch and pumpkinseed are probably the most abundant species in the river. Other common species are the white sucker, black crappie, golden shiner (*Notemigonus crysoleucas*), spottail shiner, and bluntnose minnow (*Pimephales notatus*) (Dunning et al. 1978).

The habitat of fishes of the St. Lawrence River changed considerably after hydroelectric development. Historical spawning sites for walleyes and lake sturgeon (*Acipenser fulvescens*) were inundated or altered by construction of the Moses–Saunders Dam, which also limits spawning migrations. In addition, numerous dams on major tributaries (the Oswegatchie, Grasse, Raquette, and St. Regis rivers) reduced spawning runs of many other species.Spawning by longnose gar, mooneye (*Hiodon tergisus*), and channel catfish were historically recorded in the river but have not been documented recently. A tagging study by Eckert and Hanlon (1977) indicated random and unpredictable movement throughout the St. Lawrence River.

Recent survey data have indicated a severalfold decline in trap nets CPUE in the upper section of the river between 1974 and 1985 (Hart 1986). McCullough (1986), who analyzed standardized gill net survey data collected after 1977, found a threefold variation in abundance among years for northern pike, smallmouth bass, yellow perch, rock bass, and pumpkinseed, but considered overall abundance to be stable in the study area.

TABLE 7. The occurrence and relative abundance of 12 species of fish in the St. Lawrence River over five decades (R = rare, U = uncommon, M = moderately common, C = common, A = Abundant, O = not known to occur, and — = no information). From Patch and Busch (1984).

Species	1930's	1940's	1950's	1960's	1970's
Lake sturgeon[a]	M	M	M	U	R
Northern pike	A	C	C	M	C
Muskellunge[b]	M	—	—	U	U
Brown bullhead	A	A	A	A	A
White perch	O	O	O	O-R	C
Rock bass	A	A	A	A	A
Pumpkinseed	A	A	A	A	A
Bluegill	R	R	U	U	U
Smallmouth bass	C	C	C	C	A
Largemouth bass	M	M	M	M	M
Yellow perch	A	A	A	A	A
Walleye	C	C	—	U	U

[a] *Acipenser fluvescens*.
[b] *Esox masquinongy*.

TABLE 8. Major food preferences of the dominant sport and commercial (SC) and forage species of fish in the St. Lawrence River. Data from Sibley and Rimsky-Korsakoff (1931) and Ringler (1977).

Zooplankton	Benthos	Fish
Forage fishes	Forage fishes	SC species
Mimic shiner	Spottail shiner	Northern pike
Emerald shiner	Logperch	Smallmouth bass
Juvenile yellow perch	Mottled sculpin	Walleye
	Bluntnose minnow	Largemouth bass
SC species		
Alewife	SC species	
Lake whitefish	Yellow perch	
	Rock bass	
	Pumpkinseed	
	White sucker	
	Brown bullhead	
	White perch	
	Black crappie	

Fish Harvest

During 1975-81, the Michigan sport fishery on the St. Marys River consisted of some 11 000 anglers who fished about 100 000 anglers days in the river annually. About 14 % of the effort was directed at salmon, trout, and lake whitefish (*Coregonus clupeaformis*), and 86 % at other species — mainly northern pike, smallmouth bass, walleyes, yellow perch, suckers, brown bullheads, and sunfishes. The number of angler days directed toward salmonids has increased in recent years (Koshinsky and Edwards 1983). Angling effort in the St. Marys River may be apportioned loosely as follows: 10 % above the locks, 40 % in the developed area at St. Marys Rapids, and 50 % downstream from the rapids (Koshinsky and Edwards 1983).

Average catches in the rapids area were roughly 0.1 fish per angler hour — lower than in the rest of the river, where the average in recent years has been about 0.5 fish per hour (Koshinsky and Edwards 1983). Tag-and-recapture studies of St. Marys River fish have indicated that anglers, over a period of several years, sometimes harvest a significant percentage of certain species (Liston and McNabb 1986a): two years of monitoring indicated a recapture rate of about 28 % for smallmouth bass, 26 % for northern pike, 10 % for walleye, and 9 % for yellow perch.

The Canadian sport fishery on the St. Marys River has been assessed principally in the Rapids area of Sault Ste. Marie, although a sport fishery is also present throughout the river. Creel census studies in the Canadian Rapids area (data combined for 1971, 1972, 1976, 1977, and 1982) indicated that anglers caught the following species in decreasing order: lake whitefish, rainbow trout (*Salmo gairdneri*), other trouts e.g. brook trout (*Salvelinus fontinalis*), splake (lake trout × brook trout), lake trout (*Salvelinus namaycush*), panfish, sucker, walleye, coho salmon (*Oncorhynchus kisutch*), pink salmon (*O. gorbuscha*), northern pike or muskellunge (combined), chinook salmon (*O. tshawytscha*), burbot, and a few others (Koshinsky and Edwards 1983).

Winter sport fishing adds significantly to the overall recreational use of the St. Marys River. Gleason and Behmer (1975) concluded that the walleye fishery in Munuscong Bay in 1974–75 was the most important recreational winter ice fishery on the river.

No commercial fishing is permitted on the St. Marys River. The Chippewa–Ottawa Treaty Fishery Management Authority allows subsistence fishing, but not commercial fishing. Species taken by subsistence fishermen in the river include trouts, lake whitefish, round whitefish (*Prosopium cylindraceum*), lake herring (*Coregonus artedii*), walleye, yellow perch, suckers, burbot, northern pike, salmons, catfishes (*Ictalurus*), and smallmouth bass.

During 1983–84, anglers expended an estimated 1.6 million h of effort in the St. Clair River and 2.82 million h in the Detroit River (Haas et al. 1985). The average catch per hour was 0.24 in the St. Clair River and 1.01 in the Detroit River. The ratio between the Detroit River and the St. Clair River was 1.74 for angler effort, 7.38 for catch, and 4.21 for CPUE. The differences between rivers are attributed to migrations from Lake Erie and to the selectivity of Detroit River anglers. Angling effort from shore has remained nearly constant over a 30-yr period, whereas that from boats has increased substantially.

Estimated annual angler effort (hours per hectare) for all species was 281 in the St. Clair River and 239 in the Detroit River. These rivers provide a substantial amount of recreation when compared with the average annual sport fishing effort on inland lakes of 94.1 $\text{h}\cdot\text{ha}^{-1}$ (Colby et al. 1979).

An estimated 67 fish weighing a total of 32 kg were harvested per hectare annually in the St. Clair River; for the Detroit River these estimates were 241 fish and 74 kg. The average annual harvest of walleyes from Michigan waters was estimated to be 26.7 $\text{kg}\cdot\text{ha}^{-1}$ in the St. Clair River and 15.3 $\text{kg}\cdot\text{ha}^{-1}$ in the Detroit River — considerably higher than most other estimates reported in the literature. Colby, et al. (1979), who summarized available studies of walleye biology and yield, determined that "good walleye waters" yield about 5 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ to anglers.

Most of the harvest by anglers in Ontario waters of the lower Detroit River has been composed of white bass and walleye in the summer boat fishery. These species were usually taken in temporally discrete fisheries — white bass being in May and June and walleye in July and August. Although the CPUE for walleye has varied over the years, it remained stable in 1975–83, ranging from 0.134 to 0.175 fish•angler h^{-1}, or from 26 000 to 30 000 fish (Sztramko and Paine 1984). During 1956–80, the variation in CPUE for white bass was more pronounced (0.170–1.540 fish•angler h^{-1}). Total estimated effort remained stable after 1976, ranging from 120 169 to 159 465 angler h. Other species harvested included yellow perch, freshwater drum, rock bass, and smallmouth bass.

It was estimated that the annual angler harvest of fish per kilometer of stream was 6 471 fish or 3 046 kg in the St. Clair River and 58 841 fish or 15 549 kg in the Detroit River. Hesse and Newcombe (1982) estimated the total abundance of six of the major species in two channelized segments of the Missouri River to be 1 870 and 13 087 fish•km^{-1}. Risotto and Turner (1985) estimated mean annual commercial harvest (kilograms per kilometre of stream) to be 4 577 in the Mississippi River, 2 915 in the Ohio River, and 449 in the Missouri River.

Fish tagging studies in the St. Clair and Detroit rivers during 1983–85 included 43 species of fish (Haas et al. 1985); of these, 13 were recovered in sufficient quantities to enable rough estimates of movement through the SCDRS and even into Lakes Huron and Erie. Average distances moved and rates of travel were highest for walleyes and white bass. Tagged walleyes have shown substantial movement from Lake Erie into the SCDRS in spring and back to Lake Erie in fall or winter (Wolfert 1963; Ferguson and Derksen 1971; Michigan Department of Natural Resources, Mt. Clemens, MI, unpubl. data). Yellow perch, channel catfish, freshwater drum, and white sucker also showed a strong tendency to move between the St. Clair and Detroit rivers and the adjacent Great Lakes. These observations support an assertion that the high productivity of the St. Clair and Detroit rivers sport fisheries is partly due to migrations of fish stocks from the adjacent Great Lakes.

The earliest record of commercial fishing in the SCDRS was the seining of lake whitefish in about 1830 at Ecorse, Michigan, in the Detroit River. In the 1880s, commercial seiners operated no less than 30 stations, extending from the head to the mouth of the Detroit River. Eight species of fish were dominant in the harvest: lake whitefish, lake herring, walleye, lake sturgeon, largemouth bass, muskellunge, northern pike, and common carp. Most of the fishery was carried out in fall, usually from early October to early December. The yield of the two prominent species, lake whitefish and lake herring, was fairly high from 1871 to 1890. In about 1890, however, the lake herring harvest ceased on the Canadian side of the Detroit River and there was a coincident decrease in the harvest of whitefish. Whitefish harvest increased slightly until 1913, but then collapsed in about 1920. Lake herring and lake whitefish migrated into Lake St. Clair from western Lake Erie by way of the Detroit River, principally in fall. It was speculated that declines in the 1890s were partly due to the extensive fishery for these species in the Detroit River and Lake St. Clair (Wakeham and Rathbun 1897), and not to the discharge of sewage into the Detroit River.

The decreased catch of lake whitefish in the U.S. waters of western Lake Erie and the Detroit and St. Clair rivers in about 1870 heightened interest in artificial propagation, which had been pioneered in Europe several decades earlier (Todd 1986). A number of private hatcheries were established in the area, particularly along the western basin of Lake Erie in Ohio near Toledo, Cleveland, and Sandusky. Canada opened a hatchery at Sandwich (Windsor) on the Detroit River in 1876 and Michigan soon built one at Detroit. The lake whitefish was the first species propagated in these hatcheries in numbers large enough for planting in Lake Erie and its interconnecting channels and tributaries. The introduction and expansion of hatcheries to meet declines in important species resulted in increased resistance to other conservation measures — especially restriction on fishing.

In the late 1800's and early 1900's, walleye still ranked second in market preference and fishermen actively sought spawning aggregations. For a number of years after 1880, personnel of the Sandwich hatchery collected eggs from ripe walleye at Bois Blanc Island and other locations in the Detroit River. It may therefore be inferred that spawning runs once occurred there, but were either small or did not persist long. The Detroit hatchery sometimes obtained walleye eggs from the Canadian side of the St. Clair River — suggesting that walleye runs to the American shores near Detroit were also small, as mentioned by Goode (1884).

Gallagher and Van Oosten (1943) reported that a number of species declined in the Detroit River in the 1940's. Although the Canadian catch of most species had diminished, it is not safe to assume on this basis alone that the fish were less abundant than formerly. Such species as lake whitefish, lake herring, lake sturgeon, and walleye may have been prevented from migrating into Lake St. Clair by the pollution of the Detroit and St. Clair rivers. The destruction of spawning grounds during channel dredging may have also been a factor (Smith 1917). According to testimony presented to the International Board of Inquiry in 1939 and 1940 (Gallagher and Van Oosten 1943), "Pollution was once and in certain waters still is, a serious menace to fish particularly in the Detroit and St. Clair rivers". Effluents from municipal sewers, steel mills, oil refineries, paper mills, alkali plants, and sugar plants — together with oily wastes from vessels — were held responsible for either killing fish directly or destroying their spawning and feeding grounds.

The fisheries of the St. Clair River were small in the 1890's. The principal fishing centers in Michigan were at Roberts Landing, Marine City, St. Clair, and Algonac. Few haul seines were used; hand and troll lines were used to capture walleye primarily. Although the walleye was the main species harvested, yellow perch, northern pike, and lake sturgeon were also taken in Ontario waters. Largemouth bass were also taken by seines in the 1890's. The runs of Lake Erie lake whitefish far up the St. Clair River failed long before the turn of the century (Geare 1884), and presumably before pollution could be blamed for the decline. Few lake whitefish entered Lake St. Clair, the Detroit River, or Michigan waters of Lake Erie after 1920 (Koelz 1926).

In the St. Lawrence River, 5 % of 23,200 fish tagged in the spring of 1976 were recaptured over a 4-mo period (Eckert and Hanlon 1977). Brown bullhead made up 76 % of the total recaptures, followed by black crappie (10 %) and yellow perch and smallmouth bass (4 % each). Percent returns, by species, closely reflected the percent tagged. The significance of the spring fishery for brown bullhead and black crappie had not been previously demonstrated. However, northern pike and yellow perch were the most important species in terms of angler preference and harvest.

Canadian commercial catch statistics, which include most of the international section of the St. Lawrence River, has been gathered since 1924 (Patch and Busch 1984). Despite minor fluctuations in total catch in the early years, no major decline developed until 1938, when the catch dropped below 9.1 t and remained there until 1943. Lake sturgeon, American eel (*Anguilla rostrata*), northern pike, and catfish dominated the catch during these years, along with a large group of fish of unspecified species (about 50 % of catch). Catches increased steadily through 1950, then rapidly declined, even though annual landings averaged 158.8 t in the 1960's and 1970's. Common carp, bullhead, sunfish, and yellow perch dominated the catch during the 1960's. Common carp composed 56 % of the catch in 1970, but declined steadily to negligible amounts by 1980. Yellow perch, sunfish, and bullhead dominated the catch throughout the 1970's.

The Canadian commercial catch of yellow perch from the St. Lawrence River was as high as 53 t (in 1979). Catches have ranged from 4 t in the 1940's to 29 t in the 1970's. Walleye landings never exceeded 2 t and were <0.5 t in the 1970's. Annual northern pike landings occasionally exceeded 3 t in the 1930's but have rarely exceeded 0.2 t in recent years. The once thriving commercial fishery for lake sturgeon flourished in the mid to late 19th century, but then collapsed in the 1890's and has never recovered. Catches for this species in the 1930's and 1940's rarely exceeded 4 $t \cdot yr^{-1}$ and have been as low as 0.2 t in recent years.

Food Web Dynamics

Aquatic macrophyte beds play a central role in the food web of the St. Marys River, and probably in the other connecting rivers where food web dynamics have not been studied in detail. Muskrats and crayfish are the principal grazers of macrophytes in emergent and submersed wetlands. Analysis of aerial photographs of emergent wetlands densely populated with muskrat have shown that even at the maximum density observed, the muskrats grazed only a small fraction (<3 %) of the annual standing crop of fresh plant material. SCUBA-assisted mapping of 19.8 km of submersed wetlands on the river bottom showed that crayfish grazing was localized and suggested that crayfish graze an equally small fraction (<3 %) of the annual standing crop of plants. Most vegetation appears to enter the food web as detritus.

The breakdown of submersed macrophytes provides the St. Marys River with an important source of food. Detritus and associated microorganisms come as a pulse in July and early August, from the mineralization of macrophytes produced the previous year. About 20 g $AFDW \cdot m^{-2}$ of labile (usable) organic plant material is mineralized by early August. Similarly, emergent wetlands are pulsed with labile detritus originating from shoots and associated microorganisms of decomposition, in May and June each year. Dead shoots are retained in emergent wetlands over winter. Some small fraction of the dead shoots (about 10 %) is exported downstream at ice breakup, before new emergent shoots develop in the wetlands to arrest shoot movement. As water temperature rises in the wetlands in spring (April–May), decomposition of dead shoots from the previous year accelerates. A rich supply of labile detritus is produced until June. Dead shoots are completely broken down by about the end of June; the more refractory portions of shoots join refractory detritus from previous years on the sediment surface.

In contrast, the rootstocks of emergent plants are recycled in the sediment with little apparent output of detrital biomass to the food web. During winter, and accelerating with increasing hydrosoil temperature in early summer (particularly in June and July), rootstocks of the previous growing season die back. Partly decomposed rootstock fragments carried over from previous years also decompose rapidly during this time. In this die-back and decomposition process, some 880 g $AFDW \cdot m^{-2}$ of rootstock material becomes detritus, of which 95 % decomposes in a 4-wk period beginning about mid-June. This rootstock decomposition coincides with the period of accelerated shoot growth in the wetlands. The conservative cycling of plant nutrients in the clay rootstock zone may release nutrients that support the development of new shoots.

The organic material provided by decaying emergent macrophytes in spring may be used by benthic microinvertebrates (cladocerans and copepods), as suggested by their dramatic increases in abundance in these emergent wetlands during May (Duffy 1985). Although the standing stock of these small copepods and cladocerans is low, each has rapid turnover time. Outside emergent wetlands, zooplankton seemingly responds more clearly to the production of phytoplankton than to the production of macrophyte detritus. Open-water zooplankton is dominated by copepods during most of the year (Selgeby 1975; Thomas and Liston 1986). However, cladocerans are common in July and August, when the entire zooplankton increases numerically in response to increased phytoplankton concentrations.

Soft-bottom benthic organisms outside the aquatic macrophyte zone respond to the food provided by phytoplankton and by the breakup of submerged macrophytes from August to October, both numerically and in biomass. The organisms completing development in spring, such as the previous year's cohort of *Hexagenis limbata*, also show rapid growth in spring — which may be related to the seasonal export of detritus from emergent wetlands. In the emergent wetlands, benthic macroinvertebrates increase numerically and in biomass during the period of maximum periphyton production in August and September.

Within wetlands, much of the substrate is anaerobic below the first few centimeters; thus few benthic organisms use rootstock production. At the wetland edge and in *Isoetes* meadows offshore, almost every plant has at least one large oligochaete (Haplotaxidae) associated with the root system. These worms most likely use the rootstock production when dissolved oxygen is not limiting.

Different macroinvertebrate functional groups contribute various amounts to community production in several habitats of the St. Marys River (Duffy et al. 1987). Collector organisms (burrowing mayflies and clams) dominate the production in offshore soft-bottom communities of Lake George, whereas predators such as odonates, hemipterans, and beetles contribute substantially to the production in the emergent wetlands. In Lake Nicolet, collector organisms also contribute to the production in both habitats. Shredder organisms are also important in Lake Nicolet and include organisms such as *Hyalella azteca*, *Asellus*, and *Lirceus*. In the rapids area, collectors (net-spinning caddisflies), shredders (crayfish), and scrapers (heptageniid mayflies) all contribute significantly to annual production. These differences in biomass production largely reflect differences in hydrology and basin morphometry. Because Lake George is wider and deeper than Lake Nicolet, fine particulate matter settles out to support a community that can use it. On the other hand, the much narrower and shallower Lake Nicolet receives most of the upper river discharge, and fewer fine particles settle out; consequently shredders and collectors predominate there.

The stomachs of many young-of-the-year and adult forage fish (yellow perch, spottail shiner, emerald shiner, mimic shiner) in the St. Marys River contained large quantities of macroinvertebrates (Braun 1982; Sweet 1982). Furthermore, several forage species, including these three shiners, plus the bluntnose minnow and common shiner (*N. cornutus*), had large amounts of detritus in their alimentary tracts (Sweet 1982). Many important forage fish species (rainbow smelt, spottail shiner, trout-perch, logperch, and others) fed primarily on macroinvertebrates in the St. Marys River (Sweet 1982; Dexter 1983). Of greatest importance to most fish were chironomids, which also constituted the most abundant macroinvertebrate taxon collected. Trichoptera, Ephemeroptera, and Amphipoda were also important, but varied with fish species and season. Densities of these organisms were greatest in the macrophyte beds of the upper and lower littoral zone. The rainbow smelt is the forage fish most commonly consumed by piscivores in the St. Marys River System. Another important finding is the prevalence of large mayflies (*Hexagenia* and *Ephemera*) in the diets of yellow perch and lake herring. In early summer, during the 2-wk period when *Hexagenia* and *Ephemera* are emerging, these insects are the single most important item in the diet of lake herring. Burrowing mayflies are also eaten by gulls, terns, other birds, fish, and invertebrates (e.g. adult odonates). Crayfish populations are known to be high in some areas of the St. Marys River, and provide important forage for yellow perch, smallmouth bass, and rock bass (Joyce 1983; Boregeson 1983).

Northern pike and walleyes fed primarily on rainbow smelt; spottail shiner and trout-perch were of secondary importance. Diet studies by Kapaun (1981) and Boregeson (1983) indicated that 15 species of fish were the prey of northern pike in the St. Marys River. Of these, rainbow smelt, spottail shiner, and trout-perch were most important in open-water seasons, and sculpins (*Cottus* spp.) and white sucker in winter.

Adult walleye ate primarily rainbow smelt, though trout-perch and spottail shiner were also important (Sargent 1982; Joyce 1983). Young-of-the-year perch were also a primary food of juvenile walleye and northern pike (Boregeson 1983; Kapaun 1981). Where young-of-the-year yellow perch are known to be an important food of walleye, they may determine walleye year-class success by reducing cannibalism (Forney 1976; Ney 1978). The lack of emerald shiner (one of the most abundant minnows in the St. Marys River) in the diets of major predators was surprising, but may be a function of time, temperature preference or collection methods (Liston and McNabb 1986a).

Young yellow perch relied heavily on zooplankton, although mayfly nymphs became increasingly important in volume for larger young-of-the-year perch (McNitt 1982). Mayflies (especially *Hexagenia* spp.) were eaten by older fish, though crayfish and fish were also important.

Small rock bass (<47 mm) ate crustaceans (80–87 % by volume) and insects (10–14 % by volume); arachnids (water mites) contributed a small (3–6 % by volume) though constant food source (Green 1980). Rock bass, 48–115 mm long, switched to insects such as Hemiptera, Odonata, Ephemeroptera, and Trichoptera. Crayfish were a significant food item (75 % total volume) for large rock bass (116–199 mm long) although insects were also eaten.

Most living organic carbon in the SCDRS is in the macrophyte community. About 90 % of production by submersed and emergent macrophytes and periphyton is produced in the broad and shallow lower portions of both rivers — that is, below Russell Island in the St. Clair River and Fighting Island in the Detroit River. Zooplankton typically dominates the primary consumer level of production, particularly in the Detroit River. Differences between areas in standing crops of primary producers and consumers usually reflect increasing eutrophication from headwater to mouth, but it may also reflect the quantity and quality of habitat, and sometimes the very limited data. Accuracy of the various estimates needs to be explored.

In many small to medium-size streams, allochthonous leaves and other material are an important source of energy. The quantity of organic matter (leaves and adult insects) that reaches the SCDRS is unknown so estimates were based on data gathered by Virginia Polytechnic Institute & State University (VPI 1985) and Gasith and Hasler (1976). The VPI (1985) study determined that the average annual accumulated input of leaves and insects over the entier surface of the Kanawha River, West Virginia was 8.0 g AFDW$\cdot$m^{-2} and 0.68 g AFDW$\cdot$m^{-2}, respectively. For Lake St. Clair we used an annual average value of 690 g AFDW of leaves per meter of wooded shoreline (Gasith and Hasler 1976). Annual average deposition of insects into Lake St. Clair was set at 25 g AFDW$\cdot$m^{-2} at the shoreline (VPI 1985), and decreased linearly out to 13 m. An average was taken and was applied to a 13-m wide band aroung the lake. All estimates were scaled down to adjust for differences in river widths, and amount of wetlands and industrial areas associated with various sections of the river. Estimated annual additions of leaves and adult insects into the St. Clair River, Lake St. Clair, and Detroit River was 144, 90 and 260 t, respectively. These values may be underestimates since they do not include storm sewer effluents from metropolitan areas. Direct sewage effluents to the connecting rivers were estimated from STORET retrieval of data for the 1984 water year (Table 3).

Another aspect of food chain dynamics of flowing water is movement of phytoplankton and zooplankton through the rivers as drift. Instantaneous standing crop of plankton is small, compared with that of the other stationary primary producers and consumers (Table 3). However, if one calculates the amount of plankton passing over a square meter of bottom, the figure equals or exceeds production of some of the stationary producers — particularly in the rivers. The annual estimates in metric tons (AFDW) of drift passing through the St. Clair River, Lake St. Clair, and Detroit River, respectively, are as follows: phytoplankton 10 860, 43 360, and 27 960; and zooplankton 13 620, 29 900, and 19 280.

Dissolved organic matter (DOM) and particulate organic matter (POM) are known to exceed by many times the amount of organic matter of the living plankton, macrophytes, and benthic fauna. The only DOM measurements available, from Lake Huron, average 2.7 g•m^{-3} (Robertson and Powers 1967). The amount of POM coming into the SCDRS from Lake Huron may be about 0.7 g•m^{-3} (Robertson and Powers 1967); an average of 1.4 g•m^{-3} was measured at the mouth of the St. Clair River, and up to 2.0 g•m^{-3} in Lake St. Clair (Leach 1972). A single sample from the mouth of the Detroit River measured 3.8 g•m^{-3} (Robertson and Powers 1967). Suspended solids increased by a factor of six between Lake Huron and Lake Erie (Kauss and Hamdy 1985).

Estimates of fish standing crop (kg•ha^{-1}•yr^{-1} wet weight) were 480 in the St. Clair River, 130 in Lake St. Clair, and 190 in the Detroit River. These estimates were derived by applying a 10 % conversion to total primary production (Odum 1971). A turnover ratio of 0.6 was to estimate standing crop. These estimates include the biomass of both sport and non-sport fish species and are in the range of standing crops reported for southern reservoirs (Rainwater and Houser 1982) and for a variety of inland waters (Waters 1977). Sport fish harvest in the St. Clair River (32 kg•ha^{-1}) amounts to 7 % of the total estimated fish biomass in the St. Clair River, and harvest (74 kg•ha^{-1}) in the Detroit River amounts to 39 % of the total fish biomass. The difference may partly reflect the selectivity of the Detroit River anglers, but may also involve the large influx of sewage treatment by-products (Table 3). If energy from sewage is considered available through trophic transfer, the standing crop of fish would be 360 kg•ha^{-1} wet weight and the harvest would amount to only 20 % in the Detroit River. Fish production estimates based on trophic conversions from the primary consumer level to fish were 66 % lower than those based on the primary producer level for the St. Clair River, about equal in Lake St. Clair and about 36 % lower in the Detroit River.

In the St. Lawrence River the importance of submersed macrophytes was documented by Mills et al. (1981). Raynal and Geis (1978) reported the presence of a loose layer of whole or fragmented plants along bottom irregularities at 4–5 m depths during winter. Mills et al. (1981) found a diverse benthic invertebrate community associated with these detrital "windrows", nearly 3.5 times more invertebrates being associated with these vegetation mats than with adjacent barren areas. Within the vegetative mats, gastropods and amphipods dominated the invertebrate biomass, which totaled nearly 11 g AFDW•m^{-2}, or about six times the standing crop of peripheral substrates.

The distribution and abundance of benthic invertebrates in the St. Lawrence River largely reflect the available food sources, as modified locally by current flow and substrate characteristics (Mills et al. 1981). Mollusks dominate the upper section of the river in response to the large influx of plankton from Lake Ontario. Robertson and Powers (1967) reported that particulate organic matter at the headwaters of the St. Lawrence River measured during a single period in summer in 1966, was 1.68 g AFDW•m^{-3}. Dissolved organic matter was 5.98 g AFDW•m^{-3}. As the particulate matter is filtered or settles out downstream (Mills and Forney 1982), the fauna is replaced by coarse detrital feeders such as amphipods and snails, which feed on the large detrital pool provided by the annual fall die-off of macrophytes. This transition is most obvious in flowing-water offshore areas, whereas substrate and related periphyton growth may override this downstream trend in shallow-water areas.

Benthic invertebrates appear to be the dominant component in the food web leading to fish in the connecting rivers. We realize that the diets of fishes rarely remain constant throughout their development; larvae of all fish species feed on zooplankton, juveniles feed on benthos for varying lengths of time, and opportunistic adult piscivores occasionally feed heavily on invertebrates. However, chironomids and amphipods were two of the foods eaten most often by juvenile fish in the St. Lawrence River (Johnson 1983). Likewise, benthos was preferred (Table 8) by adult sport, commercial, and forage species in the St. Lawrence River (Sibley and Rimsky-Korsakoff 1931; Ringler 1977).

Allochthonous input of terrestrial leaves and insects to the St. Lawrence River (2 540 t•yr^{-1}, Table 3) is higher than in the other connecting rivers because of the presence of forested wetlands and the cumulatively extensive shorelines of the many small islands (Patch and Busch 1986). We estimated length of shoreline within each river section including that associated with the islands. We estimated annual inputs from the 620 ha of forested wetlands as 320 g AFDW•m^{-2} of leaves and 25 g•m^{-2} of insects. We assumed that 46 % of the shoreline was wooded, judging from descriptions by Patch and Busch (1986), and derived the average deposition rate as we did for Lake St. Clair.

Cooley (1978) provides an overview of the biological data collected through 1978 on the St. Lawrence River and conceptualized the food webs for three areas, shallow, deep, and wetland zones. His outline of the flow of energy appears reasonable but standing stock and production estimates are summer values only, and none have been expanded to encompass a river wide approach. However, he does suggest the mapping of ecological zones as an aid in evaluating the overall production of various components of the river.

Conclusion

Our review of standing crop and production for each trophic level of the connecting rivers of the Great Lakes, points out the paucity of available empirical data for some biological compartments, especially periphyton and zooplankton. These identifications of data gaps and the summary of other information that preceded should serve as a starting point for future research on productivity in the connecting rivers of the Great Lakes. Once values are determined from actual sampling of these systems (rather than from the literature), workers should be able to estimate the flow of material between components of the ecosystem by using the 10 % rule or by using more refined modeling techniques. The precision required will depend on the questions asked.

Production estimates given in Table 3 appear to be in the correct order of magnitude. Easily measured and interpreted variables such as phosphorus, chlorophyll *a* (Table 1), and POM (Robertson and Powers 1967) increase 3–5-fold from the St. Marys River to the St. Lawrence River. Communities that are dependent on nutrients in the water column, such as phytoplankton, periphyton, and zooplankton simi-

TABLE 8. Major food preferences of the dominant sport and commercial (SC) and forage species of fish in the St. Lawrence River. Data from Sibley and Rimsky-Korsakoff (1931) and Ringler (1977).

Zooplankton	Benthos	Fish
Forage fishes	Forage fishes	SC species
Mimic shiner	Spottail shiner	Northern pike
Emerald shiner	Logperch	Smallmouth bass
Juvenile yellow perch	Mottled sculpin	Walleye
	Bluntnose minnow	Largemouth bass
SC species		
Alewife	SC species	
Lake whitefish	Yellow perch	
	Rock bass	
	Pumpkinseed	
	White sucker	
	Brown bullhead	
	White perch	
	Black crappie	

larly increase through the system. Other extensive studies on the Great Lakes (Vollenweider et al. 1974; Watson and Carpenter 1974) show production was estimated reasonably well for each of the connecting rivers.

Estimates of fish production presented here are admittedly simplistic, but if these estimates are reasonably accurate, they would place the Great Lakes connecting rivers among the more productive waters of the world (see Backiel and Penczak 1989; Randall et al. 1989; Welcomme 1985). These rivers have a good balance of autochthonous and allochthonous production with an extensive littoral area (60 % <3.7 m), excellent water quality, and cultural enrichment levels which for the most part have maintained a balance between autotrophic and heterotrophic food chains. We have noted that some of the fish biomass and yield in the connecting rivers is contributed by migrants from the Great Lakes proper, particularly in the SCDRS. However, one must remember that the SCDRS provides a major subsidy of drifting invertebrates and POM into Lake Erie, which is returned to the rivers in the form of migrating fish.

We highlighted the relative contribution of various producers and consumers between rivers. Relative contribution depends on water chemistry, basin topography and various man-induced impacts. Standing crop of emergent macrophytes is similar across all rivers, reflecting the universal effectiveness of macrophytes in tapping into relatively large nutrient pools within the sediments and the atmosphere. Consequently, in the nutrient poor waters of the St. Marys River, emergent macrophytes are an important source of organic matter (67 % primary production) — in contrast to the more enriched St. Lawrence River where phytoplankton dominates (76 %). The physical setting of the St. Clair River delta is unique and the emergent macrophyte production there (>80 000 t AFDW) far exceeds that in any of the other connecting rivers. One can only imagine the extent of emergent beds in the lower Detroit River before the area was industrialized. Some of the production of emergent macrophytes has probably been replaced by that of submersed macrophytes, but more likely has been replaced or exceeded as a result of sewage inputs from Metropolitan Detroit. Regardless of any local limiting factor, the submersed and emergent macrophytes and associated periphyton are a major storehouse of organic matter in the connecting rivers.

Macrophytes not only produce large quantities of organic matter, but are the principal remaining physical structure in parts of the connecting channels, since debris is removed during channel maintenance. Aquatic macrophytes help retain particulate organic matter in river systems by immediate trapping in plant beds and long-term storage in root systems. The magnitude of autochthonous production in littoral areas and any change in taxonomic composition should receive more attention. Without this information, a full understanding of fish production in the connecting river is not possible.

The biomass of macrophytes and periphyton is also probably retained by the connecting rivers more efficiently than phytoplankton — e.g. by creating a tighter spiral, as described by Elwood et al. (1983). Spiral length is defined as the average distance between entry of POM into the system and its oxidation. Once in the spiral, this material is processed or degraded by the respiration of associated microflora, leached of its dissolved organic matter, captured and consumed by biota, and incorporated into the sediments. Although dead and dying macrophytes and periphyton may be scoured or sloughed into the drift and moved through the system intact, much of this material may be retained in detrital "windrows" (Raynal and Geis 1978). This tight spiral can be contrasted with plankton, which may move through the system rapidly without being used. However, Mills and Forney (1982) found significant retention of plankton in the St. Lawrence River, particularly in summer, and concluded that macrophytes may dampen current flow and act as physical strainers of plankton. They found plankton standing crop to decline about 0.5 %•km^{-1} in the St. Lawrence River. Because the St. Clair and Detroit rivers are relative short (50–60 km), similar reductions may be difficult to detect. Obviously, the shorter the system the more important the role of the stationary primary producers.

One could describe the connecting rivers by using the river continuum concept of Vannote et al. (1980). The connecting rivers have characteristics of both medium-sized streams (order 4–6) and large rivers (order>6). The autochthonous production of periphyton and macrophytes is characteristic of the middle reaches of small or medium-sized river systems, whereas phytoplankton production is characteristic of larger systems. The connecting rivers lack the organic transport from riparian sources upstream but are subsidized by high quality phytoplankton and zooplankton from the Great Lakes. These rivers are certainly autotrophic but since most of the material eventually goes through a detritus-based food web, knowledge of detrital processing and movement is critical to an understanding of the connecting rivers. An exception to the detrital pool is the periphyton component. Few data are available on periphyton, and because periphyton biomass of 10 g•m^{-2} wet weight or less is scarcely visible to the casual observer (McIntire 1973), one might assume it to be a minor component; however, McIntire's model suggested that such an assumption is false, and that low periphyton biomass may support relatively large populations of primary and secondary consumers. Intuitively one tends to associate high primary productivity with a large standing crop of plants. The compactness and availability of periphyton growth, compared with phytoplankton and its relatively high turnover, makes periphyton an extremely important source of food for consumers in the connecting rivers.

The importance of phytoplankton as a food source can be seen especially in the St. Lawrence River in relation to the high standing crop of pelecypods. Mussels proliferate similarly but less extensively in the headwaters of the Detroit River, where suitable habitat is limited by topography and bulkheading in the upper section and by pollution in the lower section. Filter feeding insects are also most abundant at the outlets of the various lakes throughout the system.

Current high water levels in the connecting channels may significantly impact aquatic vegetation although the presence of several communities on a continuum from open water to terrestrial may buffer the impact. In the St. Lawrence River the narrow-leaf meadow emergent community (tall grasses and sedges) dominated by *Carex stricta, Calamagrostis canadensis*, and *Phalaris arundinacea* are linked to the true aquatic zone only when seasonally flooded. Continued exposure to high water may produce a die-off and replacement by narrow-leaf emergents dominated by *Sparganium eurycarpum* which occurs in slightly wetter areas than the meadow community (Geis and Kee 1977). Similar successional changes may occur in submersed communities. However, replacement time is gradual and the new community biomass may be 25 % lower as found in the St. Lawrence emergent wetland by Gilmen (1976).

Compared with other rivers of the world, those of the Great Lakes are relatively unpolluted (Fremling et al. 1989; Lelek 1989); however, several polluted areas of concern remain, despite pollution abatement measures. In 1967, bottom sediments downstream from Sault Ste. Marie, Ontario, were devoid of mayfly (*Hexagenia*) nymphs, and sediments in northern Lake Nicolet supported *Hexagenia* nymphs at only low to intermediate densities (10–276$\cdot$m^{-2}) (Veal 1968). In 1973–74, zoobenthos communities extending from Sault Ste. Marie downstream to northern Lake George were severely disrupted and reduced in taxonomic diversity by increases in oil, phenol, cyanide, and toxic metals (Hamdy et al. 1978; Hiltunen and Schloesser 1983). Only 4 species of worms and midges were at densities of 40$\cdot$m^{-2} in the severely polluted zone, whereas 38 species of invertebrates were present in unpolluted sediments, at densities exceeding 10 000$\cdot$m^{-2}. In 1985, pollution still limited the distribution of *Hexagenia* in this area of the river (Duffy et al. 1987). Similar pollution effects are evident in the SCDRS (Thornley 1985) and in the St. Lawrence River (Mills et al. 1981) . In addition to this area of degradation, the productivity of benthos and fish in the St. Marys River has been reduced over the past 30 years by the dewatering of 25 ha of the St. Marys Rapids and Whitefish Channel (Koshinsky and Edwards 1983).

Taxonomic composition within several of the aquatic communities varies little over the 4 latitude degrees and 10 longitude degrees separating the connecting waters. The diatom genera *Cyclotella, Asterionella, Fragilaria, Stephanodiscus*, and *Melosira* are dominant throughout the system. The zooplankton species *Diaptomus sicilis* and *Cyclops bicuspidatus* predominate in the St. Marys River and *C. bicuspidatus, D. minutus*, and *Bosmina longirostris* in the rest of the system. The submersed macrophytes *Isoetes* and *Chara* dominate the St. Marys River, *Chara* and *Vallisneria* the SCDRS, and *Myriophyllum* and *Nitellopsis* the St. Lawrence River. The taxonomic composition of periphyton is not well documented but diatoms appear to dominate in the St. Marys River, followed by a gradual progression toward *Cladophora* dominance in the St. Lawrence River. Oligochaetes and chironomids numerically dominate the benthic invertebrates in all of the waters but, secondarily, mayflies are most important in the St. Marys River; mayflies plus caddisflies, gastropods, and amphipods in the SCDRS; and only amphipods and gastropods in the St. Lawrence River. *Scirpus* is the dominant emergent plant in the St. Marys River and is gradually replaced by *Typha* downstream through the system to the St. Lawrence River. Yellow perch are dominant and common in all rivers; rockbass, white sucker, walleye, and redhorse sucker are more common in the St. Marys River and SCDRS, and rockbass, pumpkinseed, and black, crappie in the St. Lawrence River.

Although several historical comparisons indicate few or no changes over the last 50 years, the introduction and spread of several exotic plants and animals is noteworthy. These include the macroalgae *Nitellopsis obtusa* (Geis et al. 1981; Schloesser et al. 1986) and *Bangia atropurpurea* (Lin and Blum 1977), the submersed macrophyte *Myriophyllum spicatum* (Schloesser and Manny 1984), and most recently the cladoceran *Bythotrephes cederstroemi* (Bur et al. 1986; Lange and Cap 1986).The white perch was first collected in Lake Ontario in the late 1940's, probably entering from the Oswego River after moving west from the Hudson River through the Mohawk River–Barge Canal System, and is now established in the lower Great Lakes (Boileau 1985). The threespine stickleback (*Gasterosteus aculeatus*) may now also be established in the upper Great Lakes, including the St. Marys River (Stedman and Bowen 1985). The spread of these species, continued introduction of exotics, the control of certain pollutants, and the recent introduction of new pollutants make the rivers dynamic, despite their large size and general stability. Monitoring such changes in biological productivity and pollution in each of these systems on a 10-yr rotating basis is strongly recommended.

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References

Backiel, T., and T. Penczak. 1989. The fish and fisheries in the Vistula River and its tributary, the Pilica River, p. 488-503. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Bailey, R. M., and G. R. Smith. 1981. Origin and geography of the fish fauna of the Great Lakes basin. Can. J. Fish. Aquat. Sci. 38: 1539-1561.

Bertram, P., T. A. Edsall, B. A. Manny, S. J. Nichols, and D. W. Schloesser. 1987. Physical and chemical characteristics of sediments in the upper Great Lakes connecting channels, 1987. (Unpubl. ms.)

Boileau, M. G. 1985. The expansion of white perch, *Morone americana*, in the lower Great Lakes. Fisheries 10(1): 6–10.

Boregeson, D. J. 1983. Food habits of selected piscivorous fish in the St. Marys River. Tech. Rep. Dep. Fish. Wildl., Mich. State Univ., East Lansing, MI. 9 p.

Braun, K. B. 1982. Food habits of the emerald shiner (*Notropis atherinoides*) the St. Marys River, Michigan. Tech. Rep. Dep. Fish. Wildl., Mich. State Univ., East Lansing, MI. 9 p.

Bricker, K. S., F. J. Bricker, and J. E. Gannon. 1976. Distribution and abundance of zooplankton in the U.S. waters of Lake St. Clair, 1973. J. Great Lakes Res. 2: 256–271.

Brown, C. L., T. P. Poe, J. R. P. French, III, and D. W. Schloesser. 1988. Relationship of phytomacrofauna to surface area in naturally occurring macrophyte strands. J. N. Am. Benthol. Soc. 7: 129–139.

Bryce, J. B. 1982. A hydraulic engineering history of the St. Lawrence Power Project with special reference to regulation of water levels and flows. Tech. Rep. Ontario Hydro, Toronto, Ont. 206 p.

Bur, M. T., D. M. Klarer, and K. A. Krieger. 1986. First records of a European cladoceran, Bythotrephes cederstroemi, in Lakes Erie and Huron. J. Great Lakes Res. 12: 144–146.

Burkholder, P. R. and W. L. Tressler. 1932. Plankton studies in some northern New York waters, p. 222–251. *In* A biological survey of the Oswegatchie and Black river systems. New York Conservation Department. Suppl. 21st Annual Rep., New York Conserv. Dep., Albany, NY.

Colby, P. J., R. E. McNicol, and R. A. Ryder. 1979. Synopsis of biological data on the walleye, *Stizostedion V. vitreum* (Mitchill 1818). FAO Fish. Synop. 119, Rome, Italy. 139 p.

Cooley, J. L. 1978. Aquatic food web characterization studies. Technical Report L. Environmental assessment of the FY 1979 winter navigation demonstration on the St. Lawrence River. Volume II. State University of New York, Institute of Environmental Program Affairs, Syracuse, NY. 17 p.

Derecki, J. A. 1984a. St. Clair River physical and hydraulic characteristics. GLERL Open File Report. Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, MI. 10 p.

1984b. Lake St. Clair physical and hydraulic characteristics. GLERL Open File Report. Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, MI. 8 p.

1984c. Detroit River physical and hydraulic characteristics. GLERL Open File Report. Great Lakes Environmental Research Laboratory, NOAA, Ann Arbor, MI. 11 p.

1985. Effects of channel changes in the St. Clair River during the present century. J. Great Lakes Res. 11: 201–207.

Dexter, J. 1983. Food habits of the trout-perch (*Percopsis omiscomaycus*) in the lower St. Marys River. Tech. Rep. Dep. Fish. Wildl., Mich. State Univ., East Lansing, MI. 12 p.

Duffy, W. G. 1985. The population ecology of the damselfly *Lestes disjunctus disjunctus* in the St. Marys River, Michigan. Ph.D. dissertation, Michigan State University, East Lansing, MI. 119 p.

Duffy, W. G., T. R. Batterson, and C. D. McNabb. 1987. The St. Marys River, Michigan: An ecological profile. U.S. Fish. Wild. Serv. Biol. Rep. 85(7.10): 138 p.

Dunning, D. J., M. J. Tarby, and J. T. Evans. 1978. Adult fisheries study. Tech. Rep. D. Environmental Assessment of the FY 1979 Winter Navigation Demonstration on the St. Lawrence River. Volume 1. State University of New York. Institute of Environmental Program Affairs. Syracuse, NY. 77 p.

Eckert, T. H., and J. R. Halon. 1977. Fisheries studies along the St. Lawrence River, p. 61–90. *In* J. W. Geis [ed.] Preliminary report: Biological characteristics of the St. Lawrence River. State University of New York. Institute of Environmental Affairs, Syracuse, NY.

Elwood, J. W., J. D. Newbold, R. V. O'Neill, and W. Van Winkle. 1983. Resource spiraling: an operating paradigm for analyzing lotic ecosystem, p. 3–28. *In* T. P. Fontaine and S. M. Bartell [ed.] Dynamics of lotic ecosystems, Ann Arbor Science, Ann Arbor, MI.

Ferguson, R. G., and A. J. Derksen. 1971. Migrations of adult and juvenile walleyes (*Stizostedion vitreum vitreum*) in southern Lake Huron, Lake St. Clair, Lake Erie, and connecting waters. J. Fish. Res. Board Can. 28: 1133–1142.

Forney, J. L. 1976. Year-class formation in the walleye (*Stizostedion vitreum*) population of Oneida Lake, New York, 1966–1973. J. Fish. Res. Board Can. 33: 783–792.

Fremling, C. R., J. L. Rasmussen, R. E. Sparks, S. P. Cobb, C. F. Bryan, T. O. Claflin. 1989. Mississippi River Fisheries, p. 309-351. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Freitag, T. M. 1984. Recent naiad molluscs of the Detroit River. Am. Malacol. Bull. 3: 105.

Gallagher, H. R., and J. Van Oosten. 1943. Supplemental report of the United States members of the International Board of Inquiry for the Great Lakes fisheries, p. 25–213. *In* Int. Board Inquiry Great Lakes Fish. Rep. Suppl.

Gasith, A., and A. D. Hasler. 1976. Airborne litterfall as a source of organic matter in lakes. Limnol. Oceanogr. 21: 253–258.

Geare, P. I. 1884. The lake whitefish, *Coregonus clupeaformis*, p. 507–540. *In* G. B. Good, [ed.]. The fisheries and fishing industry of the United States, Section I, Part III, U.S. Commission Fish and Fisheries, Washington, DC.

Geis, J. W., and J. L. Kee. 1977. Coastal wetlands along Lake Ontario and the St. Lawrence River in Jefferson County, New York. State University of New York. Institute of Environmental Program Affairs. Syracuse, NY. 130 p.

Geis, J. W., G. J. Schumacher, D. J. Raynell, and N. P. Hyduke. 1981. Distribution of *Nitellopsis obtusa* (Charophyceae, Characeae) in the St. Lawrence River: a new record for North America. Phycologia 20: 211–214.

Gilman, B. A. 1976. Wetland plant communities along the eastern shoreline of Lake Ontario. M.S. thesis. State University of New York, College of Environmental Science and Forestry, Syracuse, NY. 187 p.

Gleason, G. R., and D. J. Behmer. 1975. Navigation and winter recreation. U.S. Dep., Bur. Outdoor Recreation, Rep. Contract No. 5-18-07-02, Washington, DC. 63 p.

Glooschenko, W. A., J. E. Moore, and R. A. Vollenweider. 1972. The seasonal cycle of pheo-pigments in Lake Ontario with particular emphasis on the role of zooplankton grazing. Limnol. Oceanogr. 17: 597–605.

Glooschenko, W. A., J. E. Moore, and R. A. Vollenweider. 1973. Chlorophyll *a* distribution in Lake Huron and its relationship to primary productivity. Proc. 16th Conf. Great Lakes Res. 1973: 40–49.

Glooschenko, W. A., J. E. Moore, M. Munawar, and R. A. Vollenweider. 1974. Primary production in Lake Ontario and Erie: A comparative study. J. Fish. Res. Board Can. 31: 253–263.

Goode, B. G. [ed.]. 1884. The fisheries and fishing industry of the United States, Section I–Text. U.S. Commercial Fish and Fisheries, Washington, D.C. XXXIV + 895 p.

Goodyear, C. D., T. A. Edsall, D. M. O. Demsey, G. D. Moss, and P. E. Polanski. 1982. Atlas of spawning and nursery areas of Great Lakes fishes. U.S. Fish Wildl. Serv., Ann Arbor, MI. FWS/OBS-82/52. 164 p.

Greeley, J. R., and C. W. Greene. 1931. Fishes of the area with annotated list, p. 44–94. *In* A biological survey of the St. Lawrence Watershed (including the Grass, St. Regies, Salmon, Chateauguay systems and the St. Lawrence between

Ogensburg and the International Boundary). N.Y. Conserv. Dep. Suppl. 20th Annu. Rep. (1930), Albany.

Green, W. 1980. Food habits of the rock bass, *Ambloplites rupestris*, in the St. Marys River. Tech. Rep. Dep. Fish Wildl., Mich. State Univ., East Lansing, MI. 27 p.

Haas, R. C., W. C. Bryant, K. D. Smith, and A. J. Nuhfer. 1985. Movement and harvest of fish in Lake St. Clair, St. Clair River, and Detroit River. Final Rep. Winter Navigation Study. Mich. Dep. Nat. Resour., Fish. Div., Mt. Clemens. 610 p.

Hamdy, Y., J. D. Kinkead, and M. Griffiths. 1978. St. Marys River water quality investigations 1973–74. Ont. Min. Environ. Toronto. 53 p.

Hamdy, Y., and L. Post. 1985. Distribution of mercury, trace organics and other heavy metals in Detroit River sediment. J. Great Lakes Res. 11: 353–365.

Hart, M. L. 1986. St. Lawrence River warmwater fish assessment, p. 39–46. *In* 1986 Annual Report, St. Lawrence River Sub-committee to the Lake Ontario Committee and the Great Lakes Fisheries Commission. New York Dep. Environ. Conserv. Albany, NY.

Hatcher, C. O., and R. T. Nester. 1983. Distribution and abundance of fish larvae in the St. Clair and Detroit River. U.S. Fish Wildl. Serv., Great Lakes Fish. Lab., Ann Arbor, MI. Admin. Rep. 83-5. 41 p.

Herdendorf, C. E., S. M. Hartley, and M. D. Barnes. 1981. Fish and wildlife resources of the Great Lakes coastal wetlands within the United States. Volume 4: Lake Huron, Part 1. U.S. Fish Wildl. Serv. FWS/OBS-81/02-V4, 423 p.

Herdendorf, C. E. 1987. The ecology of the coastal marshes of western Lake Erie: A community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85(7.9). 171 p. + microfiche appendices.

Hesse, L. W., and B. A. Newcomb. 1982. On estimating the abundance of fish in upper channelized Missouri River. N. Am. J. Fish. Manage. 2: 80–83.

Hiltunen, J. K. 1978. Investigation of macrobenthos in the St. Marys River during an experiment to extend navigation through winter 1974–75. U.S. Fish Wildl. Serv., Great Lakes Fish. Lab., Ann Arbor, MI. Admin. Rep. 105 p.

1980. Composition, distribution, and density of benthos in the lower St. Clair River, 1976–1977. U.S. Fish and Wildlife Service, Great Lakes Fisheries Laboratory, Ann Arbor, MI. Admin. Rep. 80-4, 28 p.

Hiltunen, J. K., and B. A. Manny. 1982. Distribution and abundance of macrozoobenthos in the Detroit River and Lake St. Clair, 1977. U.S. Fish Wildl. Serv., Great Lakes Fish. Lab., Ann Arbor, MI. Admin. Rep. 82-2, 87 p.

Hiltunen, J. K., and D. W. Schloesser. 1983. The occurence of oil and the distribution of *Hexagenia* (Ephemeroptera: Ephemeridae) nymphs in the St. Marys River, Michigan and Ontario. Freshwat. Invertebr. Biol. 2: 199–203.

Hough, J. L. 1958. Geology of the Great Lakes. University of Illinois Press, Urbana, IL. 313 p.

Hudson, P. L., B. M. Davis, S. J. Nichols, and C. M. Tomcko. 1986. Environmental studies of macrozoobenthos, aquatic macrophytes, and juvenile fish in the St. Clair–Detroit River System. U.S. Fish. Wildl. Serv., National Fisheries Center–Great Lakes, Ann Arbor, MI. Admin. Rep. 86-7. 303 p.

Jaworski, E., and C. N. Raphael. 1976. Modification of costal wetlands in southeastern Michigan and management alternatives. Mich. Acad. 8: 303–317.

Johnson, J. H. 1983. Summer diet of juvenile fish in the St. Lawrence River. N.Y. Fish Game J. 30: 91–99.

Joyce, R. 1983. Food habits of the walleye (*Stizostedion vitreum*), sauger (*Stizostedion canadense*) and yellow perch (*Perca flavescens*) in the St. Marys River. Tech. Rep. Dep. of Fish and Wildl., Mich. State Univ., East Lansing. 9 p.

Kapaun, P. 1981. Food habits of the northern pike (Exos lucius) in the St. Marys River system. Tech. Rep. Dep. of Fish and Wildl., Mich. State Univ., East Lansing, MI. 15 p.

Kauss, P. B. 1983. Studies of trace contaminants, nutrients and bacteria levels in the Niagara River. J. Great Lakes Res. 9: 249–272.

Kauss, P. B., and Y. S. Hamdy. 1985. Biological monitoring of organochlorine contaminants in the St. Clair and Detroit Rivers using introduced clams, *Elliptio complanatus*. J. Great Lakes Res. 11: 247–263.

Koelz, W. 1926. Fishing industry of the Great Lakes. U.S. Commission on Fisheries, Report for 1925. Append. XI: 553–617.

Koshinsky, G. D., and C. J. Edwards. 1983. The fish and fisheries of the St. Marys Rapids: An analysis of status with reference to water discharge, and with particular reference to "condition 1(b)". Report to the Int. Joint Comm. 164 p + Appendices.

Kreis, R. G., Jr, T. B. Ludewski, and E. F. Stoermer. 1983. Influences of the St. Marys River plume on northern Lake Huron phytoplankton assemblage. J. Great Lakes Res. 9: 40–51.

Lange, C., and R. Cap. 1986. *Bythotrepes cederstroemi* (Schodler). (Cercopagidae: Cladocera): A new record for Lake Ontario. J. Great Lakes Res. 12: 142–143.

Larson, J. W. 1981. Essayons: A history of the Detroit District U.S. Army Corps of Engineers. U.S. Army Corps Eng., Detroit, MI. 215 p.

Leach, J. H. 1972. Distribution of chlorophyll and related variables in Ontario waters of Lake St. Clair. Proc. Conf. Great Lakes Res. 15: 80–86.

1973. Seasonal distribution, composition, and abundance of zooplankton in Ontario waters of Lake St. Clair. Proc. Conf. Great Lakes Res. 16: 54–64.

Lelek, A. 1989. The Rhine River and some of its tributaries under human impact in the last two centuries, p. 469–487. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Limno-Tech, Inc. 1985. Summary of the existing status of the upper Great Lakes connecting channels data. Limno-Tech. Inc., Ann Arbor, MI. 157 p.

Lin, C. K., and J. L. Blum. 1977. Recent invasion of a red alga (*Bangia atropurpurea*) in Lake Michigan. J. Fish. Res. Board Can. 34: 2413–2416.

Lind, O. T. 1979. Handbook of common methods in limnology. 2nd ed. C. V. Mosby Co., St. Louis, MO. 199 p.

Liston, C. R., W. Duffy, D. Ashton, T. Batterson, and C. D. McNabb. 1981. Supplementary environmental baseline studies and evaluation of the St. Marys River during 1980. U.S. Fish Wildl. Serv., FWS/OBS-80/62.1. 167 p.

Liston, C. R., C. D. McNabb, W. Duffy, D. Ashton, R. Ligman, F. Koehler, J. Bohr, G. Fleischer, J. Schuette, and R. Yanusz. 1983. Environmenal baseline studies of the St. Marys River near Neebish Island, Michigan, prior to proposed extension of the navigation season. U.S. Fish Wildl. Serv., FWS/OBS-80/62.2. 202 p. + Appendix.

Liston, C. R., and C. D. McNabb. 1986a. Limnological and fisheries studies of the St. Marys River, Michigan in relation to proposed extension of the navigation season. U.S. Fish Wild. Serv., Biol. Rep. 85(2). 764 p. + Appendices.

1986b. Environmental baseline studies during 1984 of Lake Nicolet and Munuscong Bay, St. Marys River, Michigan, in relation to proposed extension of the navigation season. U.S. Fish Wild. Serv. Biol. Rep. 86(3), Part I. 99 p. + Appendix.

Lyon, J. G. 1979. Remote sensing analyses of coastal wetland characteristics: The St. Clair Flats, Michigan, p. 1117–1129. *In* Proceedings of the Thirteenth Symposium on Remote Sensing of Environment, Ann Arbor, MI.

Magnin, E., and A. Stanczykowska. 1971. Quelques donées sur la croissance, la biomass et la production annuelle de trois mollusques Unionidae de la région de Montréal. Can. J. Zool. 49: 491–497.

Manny, B. A., D. W. Schloesser, C. L. Brown, and J. R. P. French III. 1985. Ecological effects of rubble-mound breakwater construction and channel dredging at West Harbor, Ohio (Western Lake Erie). Tech. Rep. EL-85-10, prepared by U.S. Fish Wildl. Serv. for U.S. Army Eng. Waterways Exp. Stn., Vicksburg, MS.

Marean, J. B. 1976. The influence of physical, chemical and biological characteristics of wetlands on their use by northern pike. M.S. thesis, State University of New York, College of Environmental Science and Forestry. Syracuse, NY. 175 p.

McCollough, G. B. 1985. Wetland threats and losses in Lake St. Clair. *In* H. P. Prince and F. M. D'Itri [ed.] Coastal wetlands, Lewis Publishers, Inc., Chelsea, MI.

McCullough, R. D. 1986. Annual summary, 1985 St. Lawrence River warmwater fish stock assessment, p. 39–46. *In* 1986 Annual Report, St. Lawrence River Subcommittee to the Lake Ontario Committee and the Great Lakes Fishery Commission, New York Dep. Environ. Conserv. Albany, NY.

McIntire, C. D. 1973. Periphyton dynamics in laboratory streams: a simulation model and its implications. Ecol. Monogr. 43: 399–420.

McNitt, B. 1982. Food habits of young-of-the-year yellow perch in the southern portion of the St. Marys River. Tech. Rep. Dep. Fish Wildl., Mich. State Univ., East Lansing, MI. 12 p.

Michigan Water Resources Commission. 1975. Limnological survey of the Michigan portion of Lake St. Clair, 1973. Mich. Dep. Nat. Resour., Lansing, MI. 59 p.

Mills, E. L., and J. L. Forney. 1977. Primary and secondary production in the St. Lawrence River system, p. 1–29. *In* J. W. Geis [ed.] Preliminary report: Biological characteristics of the St. Lawrence River. State University of New York. Institute of Environmental Affairs. Syracuse, NY.

1982. Response of Lake Ontario plankton entering the International Section of the St. Lawrence River. Int. Rev. ges. Hydrobiol. 67: 27–43.

Mills, E. L., S. B. Smith, and J. L. Forney. 1978. Benthic sampling and substrate analysis at ice boom sites I. Benthic invertebrate populations. Technical Report B. Environmental Assessment of the FY 1979 Winter Navigation Demonstration on the St. Lawrence River. Volume 1. State University of New York. Institute of Environmental Program Affairs. Syracuse, NY. 41 p.

1981. The St. Lawrence River in winter: population structure, biomass, and pattern of its primary and secondary food web components. Hydrobiologia 79: 65–75.

Mudroch, A. 1985. Geochemistry in Detroit River sediments. J. Great Lakes Res. 11: 193–200.

Muenscher, W. C. 1931. Aquatic vegetation of the St. Lawrence watershed, p. 121–144. *In* A biological survey of the St. Lawrence Watershed. New York Conservation Departemnt. Suppl. 20th Ann. Rep.

Muenscher, W. C. 1932. Aquatic vegetation of the Oswegatchie and Black river watersheds, p. 199–221. *In* A biological survey of the Oswegatchie and Black River systems (including also the lesser tributary streams of the upper St. Lawrence and of northeastern Lake Ontario). New York Conserv. Dep. Suppl. 21st Annu. Rep.

Munawar, M., and I. F. Munawar. 1978. Phytoplankton of Lake Superior, 1973. J. Great Lakes Res. 4: 415–422.

Muth, K. M., D. R. Wolfert, and M. T. Bur. 1986. Environmental study of fish spawning and nursery areas in the St. Clair–Detroit River system. U.S. Fish Wild. Serv., National Fisheries Center–Great Lakes, Ann Arbor, MI. Admin. Rep. 86-6. 53 p.

NALCO Environmental Sciences. 1978. Spring census of larval fishes. Technical Report 1. Environmental Assessment of the FY 1979 Winter Navigation Demonstration on the St. Lawrence River. Volume II. State University of New York. Institute of Environmental Program Affairs. Syracuse, NY. 21 p.

Ney, J. J. 1978. A synoptic review of yellow perch and walleye biology. Am. Fish. Soc. Spec. Publ. 11: 1–12.

Odum, E. P. 1971. Fundamentals of ecology. W. B. Saunders Co., Philadelphia, PA. 574 p.

Ontario Ministry of the Environment. 1979. St. Clair River organics study, biological surveys 1963 and 1977. Ontario Min. Environ., London, Ont. 90 p.

Paerl, H. W., M. M. Tilzer, and C. R. Goldman. 1976. Chlorophyll *a* versus adenosine triphosphate as algal biomass indicators in lakes. J. Phycol. 12: 242–246.

Patch, S. P., and W. N. Busch. 1984. The St. Lawrence River — past and present. A review of historical natural resource information and habitat changes in the international section of the St. Lawrence River. U.S. Fish Wildl. Serv., Cortland, NY. 340 p.

1986. Biological survey in the international section of the St. Lawrence River, with special emphasis on aquatic macrophytes, fish spawning, and macroinvertebrates. Final Report. Vol. 1. U.S. Army Corps Eng., Buffalo, NY. 305 p.

Pugsley, E. D., P. D. N. Herbert, L. W. Wood, G. Brotea, and T. W. Odal. 1985. Distribution of contaminants in clams and sediments from the Huron–Erie corridor. I. — PCBs and octachlorostyrene. J. Great Lakes Res. 11: 275–289.

Rainwater., W. C., and A. Houser. 1982. Species composition and biomass of fish in selected coves in Beaver Lake, Arkansas, during the first 18 years of impoundment (1963–1980). N. Am. J. Fish. Manage. 2: 316–325.

Randall, R. G., M. F. O'Connell, and E. M. P. Chadwick. 1989. Fish production in two large Atlantic coast rivers: Miramichi and Exploits, p. 00–00. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Raphael, C. N., and E. Jaworski. 1982. The St. Clair River Delta: A unique lake delta. Geogr. Bull. 21: 7–28.

Raynal, D. J., and J. W. Geis. 1978. Winter studies of littoral vegetation. Technical Report G. Environmental assessment of the FY 1979 winter navigation demonstration on the St. Lawrence River. Vol. 1. State University of New York. Institute of Environmental Program Affairs, Syracuse, NY. 21 p.

Rich, P. H., R. G. Wetzel, and N. V. Thuy. 1971. Distribution, production, and role of aquatic macrophytes in a southern Michigan marl lake. Freshwater Biol. 1: 3–21.

Ringler, N. H. 1977. Feeding ecology of fishes in the St. Lawrence River, p. 91–109. *In* J. W. Geis [ed.] Preliminary report: Biological characteristics of the St. Lawrence River. State University of New York. Institute of Environmental Affairs. Syracuse, NY.

Risotto, S. R., and R. E. Turner. 1985. Annual fluctuation in abundance of the commercial fisheries of the Mississippi River and tributaries. N. Am. J. Fish. Manage. 5: 557–574.

Robertson, A., and C. F. Powers. 1967. Comparison of the distribution of organic matter in the five Great Lakes, p. 1–18. *In* Studies on the environment and eutrophication of Lake Michigan. Spec. Rep. No. 30. Great Lakes Res. Div., University of Michigan. p. 1–18.

Ruta, P. J. 1981. Littoral macrophyte communities of the St. Lawrence River, New York. MS Thesis. State University of New York, College of Environmental Science and Forestry, Syracuse, NY. 73 p.

Sargent, M. 1982. Food habits of walleye (*Stizostedion vitreum*) in the St. Marys River. Tech. Rep. Dep. of Fish and Wildl., Mich. State Univ., East Lansing, MI. 12 p.

Schloesser, D. W., and B. A. Manny. 1984. Distribution of eurasian watermilfoil, *Myriophyllum spicatum*, in the St. Clair–Detroit River system in 1978. J. Great Lakes Res. 10: 322–326.

1986. Distribution of submersed macrophytes in the St. Clair–Detroit River system, 1978. J. Freshwater Ecol. 3: 537–544.

Schloesser, D. W., P. L. Hudson, and S. J. Nichols. 1986. Distribution and habitat of *Nitellopsis obtusa* (Characeae) in the Laurentian Great Lakes. Hydrobiologia 133: 91–96.

Scrudato, R. J. 1978. Benthic sampling and substrate analysis at ice boom sites. II. Heavy metals and organic content. Technical Report C. Environmental Assessment of the FY 1979 Winter Navigation Demonstration on the St. Lawrence River. Volume I. State University of New York. Institute of Environmental Program Affairs. Syracuse, NY. 16 p.

Selgeby, J. H. 1975. Life histories and abundance of crustacean zooplankton in the outlet of Lake Superior, 1970–71. J. Fish. Res. Board Can. 32(4): 461–470.

Sibley, C. K., and V. Rimsky-Korsakoff. 1931. Food of certain fishes in the watershed, p. 109–120. *In* A biological survey of the St. Lawrence Watershed. New York Conserv. Dep. Suppl. Annu. Rep.

Smith, H. M. 1917. Report of the Bureau of Fisheries. Report of the U.S. Commissioner of Fisheries for 1916. 114 p.

Stadelmann, P., J. E. Moore, and E. Pickett. 1974. Primary production in relation to temperature structure, biomass concentration, and light conditions at an inshore and offshore station in Lake Ontario. J. Fish. Res. Board Can. 31: 1215–1232.

Stedman, R. M., and C. A. Bowen. 1985. Introduction and spread of the threespine stickleback (*Gasterosteus aculeatus*) in Lakes Huron and Michigan, J. Great Lakes Res. 11: 508–511.

Strachan, W. M. J., and C. J. Edwards. 1984. Organic pollutants in Lake Ontario, p. 239–264. *In* J. O. Nriagu and M. S. Simmons [ed.] Toxic contaminants in the Great Lakes. John Wiley and Sons, New York, NY.

Sweet, D. 1982. Food habits of twelve inshore species of fish inhabiting the St. Marys River. Tech. Rep. Dep. Fish Wildl., Mich. State Univ., East Lansing, MI. 19 p.

Sztramko, L. Z., and J. R. Paine. 1984. Sport fisheries in the Canadian portion of Lake Erie and connecting waters. 1948–1980. Ontario Fish. Tech. Rep. Ser. No. 13. 43 p.

Texas Instruments. 1975. Report of fish and macrozooplankton studies on the St. Clair River in the vicinity of the proposed Belle River Power Plant. Texas Instruments Incorporated, Dallas, TX. 150 p.

Thomas, M. V., and C. R. Liston. 1986. Zooplankton composition and density in a navigation channel and near a littoral site of the lower St. Marys River, Michigan. Mich. Acad. 18: 365–373.

Thornley, S. 1985. Macrozoobenthos of the Detroit and St. Clair rivers with comparisons to neighboring waters. J. Great Lakes Res. 11: 290–296.

Thornley, S., and Y. Hamdy. 1984. An assessment of the bottom fauna and sediments of the Detroit River. Ontario Min. Environ. 48 p.

Todd, T. N. 1986. Artificial propagation of coregonines in the management of the Laurentian Great Lakes. Arch. Hydrobiol. Beih. 22: 31–50.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

Vaughan, R. D., and G. L. Harlow. 1965. Report on pollution of the Detroit River, Michigan waters of Lake Erie, and their tributaries. U.S. Dep. Health, Educa. Welfare, Public Health Serv., Div. Wat. Supply Poll. Contr., Region 5, Grosse Île, MI. 295 p.

Veal, D. M. 1968. Biological survey of the St. Marys River. Ontario Water Resour. Comm., Toronto, Ont.

Virginia Polytechnic Institute and State University (VPI). 1985. Development and application of an energy flow model to analyze impacts of navigation changes on the Kanawha River in West Virginia. Final Report. U.S. Army Corps Eng., Huntington, WV. 670 p.

Vollenweider, R. A. 1969. A manual on methods for measuring primary production in aquatic environments. Int. Biol. Prog. Handb. 12. F. A. Davis Co., Philadelphia, PA. 213 p.

Vollenweider, R. A., M. Munawar, and P. Stadelmann. 1974. A comparative review of phytoplankton and primary production in the Laurentian Great Lakes. J. Fish. Res. Board Can. 31: 739–762.

Wakeham, W., and R. Rathbun. 1897. Report of the Joint Commission relative to the presentation of the fisheries in water contiguous to Canada and United States. S. E. Dawson, Ottawa, XVI + 146 p.

Waters, T. F. 1977. Secondary production in inland waters. Adv. Ecol. Res. 10: 91–164.

Watson, N. H. F., and G. F. Carpenter. 1974. Seasonal abundance of crustacean zooplankton and net plankton biomass of lakes Huron, Erie, and Ontario. J. Fish. Res. Board Can. 31: 309–317.

Welcomme, R. L. 1985. River fisheries. FAO, Rome. 330 p. Fish. Tech. Pap. No. 262

Wells, L. 1960. Seasonal abundance and vertical movements of planktonic crustacea in Lake Michigan. U.S. Fish Wild. Serv. Fish. Bull. 60: 343–369.

Werner, R. G., and D. Ford. 1972. St. Lawrence–Eastern Ontario shoreline study. Tech. Rep. State University of New York. College of Environmental Science and Forestry. Syracuse, NY. 63 p.

Werner, R. G. 1977. Ichthyplankton and inshore larval fishes of the St. Lawrence River, p. 31–60. *In* J. W. Geis [ed.] Preliminary report: Biological characteristics of the St. Lawrence River. State University of New York. Institute of Environmental Affairs, Syracuse, NY.

Wetzel, R. G. 1975. Limnology. W. B. Saunders Co. Philadelphia, PA. 743 p.

[ed.] 1983. Periphyton of freshwater ecosystems. Dr. W. Junk Publishers. Hague, Netherlands. 346 p.

Wetzel, R. G., and G. E. Likens. 1979. Limnological Analyses. W. B. Saunders, Philadelphia, PA. 357 p.

Williams, L. G. 1963. Plankton population dynamics. U.S. Public Health Serv., Natl. Water Quality Network, Publ. No. 663, Suppl. 2.

Winner, J. M., A. J. Oud, and R. G. Ferguson. 1970. Plankton productivity studies in Lake St. Clair. Proc. Conf. Great Lakes Res. 13: 646–650.

Wolfert, D. R. 1963. The movements of walleyes tagged as yearlings in Lake Erie. Trans. Am. Fish. Soc. 92: 414–420.

Perspectives on Management of the Hudson River Ecosystem

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Abstract

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The Hudson River consists of a freshwater reach of some 257 km and an estuary of 250 km length, draining 20 917 km^2 and 12 740 km^2, respectively. Although one of the most intensively studied river systems in the world, relatively little of the information gathered to date can be used to estimate the total biological productivity of the Hudson. Further, data are insufficient for estimation of important fish stocks, their production, or their yield potentials, some of the major goals of the Large River Symposium. Nevertheless, a description of many other features such as hydrography, chemistry, and ecology is possible. Management policies for the Hudson have been largely ''event-driven'', in the sense that major anthropogenic disturbances have provided much of the focus for research, mitigation of impacts, and development of management plans. A brief history of relevant legislation, together with summaries of three major management issues of the past two decades — power plants, polychlorinated biphenyls (PCB), and a proposed highway/urban renewal project on Manhattan Island, New York City (the Westway) — offer a background of the kinds of information, uncertainties, and conflicts arising from imperfect knowledge that have characterized management to date. State-conducted fishery management programs appear to be moving toward a stated long-term goal of ''optimum sustained yield'' via an ''ecosystem approach'', although short-term programs largely do not possess the capability of implementing such an approach at this time.

Résumé

LIMBURG., K. E., S. A. LEVIN, AND R. E. BRANDT. 1989. Perspectives on management of the Hudson River ecosystem, p. 265–291. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Le fleuve Hudson se divise en un segment d'eau douce, de 257 km environ, et un segment estuarien, de 250 km environ, dont les bassins versants respectifs sont de 20 917 km^2 et de 13 740 km^2. Bien que ce réseau hydrographique soit l'un des plus intensément étudiés au monde, peu des renseignements obtenus jusqu'à maintenant peuvent servir à estimer la productivité totale de l'Hudson. De plus, les données disponibles s'avèrent insuffisantes pour l'estimation des importants stocks de poisson, de leur production et de leur rendement possible, facteurs qui comptent parmi les grands objectifs du symposium sur les grands cours d'eau. Il demeure cependant possible de réaliser une description de bon nombre d'autres facteurs, notamment ceux ayant trait à l'hydrographie, à la chimie et à l'écologie. Les politiques de gestion de l'Hudson ont, dans une large mesure, été dictées par les événements, c'est-à-dire que les importantes perturbations d'origine humaine ont en grande partie été à l'origine des travaux de recherche, de lutte contre les effets nuisibles et d'élaboration de plans de gestion. Un bref historique de la législation pertinente, présenté de pair avec des résumés des grandes questions de gestion au cours des deux dernières décennies — les centrales électriques, les biphényles polychlorés (BPC) et un projet de route et de renouveau urbain pour l'île de Manhattan (le Westway de la ville de New York) — place dans leur contexte les types d'information, les incertitudes et les conflits découlant des connaissances imparfaites qui ont caractérisé la gestion jusqu'à maintenant. Les programmes de gestion des pêches de l'État sont orientés vers un objectif à long terme de « rendement soutenu optimal » obtenu grâce à une approche par « l'écosystème », mais les programmes à court terme ne permettent pas, de façon générale, de mettre en œuvre une telle approche pour le moment.

Introduction

The Hudson River is the largest estuary/river system in the northeastern U.S, with a total length of 507 km and a drainage basin of 34 657 km^2 in five states. Most of the basin (95 %) is located in New York State, arising at Lake Tear-of-the-Clouds in the Adirondack Mountains (44°N. Lat., 74° W. Long.) and meeting the New York Bight just below Manhattan Island. Given a population of roughly 20 million, including the 10 plus million in New York City, human demands on the Hudson are many and varied. Because most of the population is concentrated in the lower estuary, the majority of environmental issues and management programs have involved this portion of the system.

One stated purpose of the Large River Symposium (LARS) is to "promote the planned development of inventory and assessment techniques and productivity models" (LARS 1985). For the Hudson, information on total system productivity, major elemental budgets, and food web quantification is far from complete, despite major data-collection efforts undertaken for environmental impact assessments. Nevertheless, studies have been conducted on many aspects of the Hudson's ecology, physico-chemical properties, water quality, geology, and so forth, and some synthesis is evidenced in recent or forthcoming publications (Limburg et al. 1986a; Barnthouse et al. 1988b). Recently, more data on ecosystem metabolism and lower trophic-level relationships has been collected (Peierls et al. 1988; Findlay et al. 1988; Pace et al. 1988; Garritt et al. 1988).

Three classes of management strategies have been employed in dealing with Hudson River environmental problems:

(1) "laissez-faire" policy dominated water pollution problems for the early part of the century;

(2) small-scale management programs have been applied to fisheries and water quality; and

(3) major management programs have consisted mainly of responses of large-scale disturbance events, usually of human origin.

The last two types of management have co-existed in the Hudson River Valley for some time and with a certain degree of overlap.

This case study will briefly describe what is known about the Hudson's natural ecosystems, and will discuss the management programs as they pertain to regional issues of the watershed.

Description of the Hudson Ecosystem

Physiographic and Hydrographic Features

From its source in the Adirondack Mountains to its confluence with the Atlantic, the Hudson carves a 507 km channel through a varied bedrock (Fig. 1). Limestone beds of Lower Devonian to Ordovician origin dominate in the north and grade into shales, slates, and dolostones farther south. The Adirondack region is an area where doming of the surface bedrock predominates. South of the Adirondacks lie the Catskills and the Wallkill and Rondout river valleys to the west, and the Berkshire and Taconic mountains to the east. A discontinuity is encountered at the Hudson Highlands, about 90 km from the estuary's mouth; here the shale belt trends to the southwest while the river uses an ancient bed to move almost straight south to join Long Island Sound. The Highlands are remnant mountains of Pre-Cambrian age and consist of mixed igneous and metamorphic rocks; the steep pass used by the Hudson is technically a fjord. From the Highlands south to New Jersey, Cambrian-Ordovician schists, gneisses, and marbles dominate, along with Triassic igneous formations. The lower basin is a part of the Ridge and Valley province which extends from Virginia up to the St. Lawrence River.

Elevation gradients range from 3.1 m·km^{-1} from the source to Fort Edward to 0.6 m·km^{-1} in the upper basin (Sanders 1982). The lower Hudson, a drowned river valley, rises only 1.5 m in its 250 km length (Klauda et al. 1980). In this reach, the estuary follows a straight, north–south path. Three large bays dominate the lower third of the estuary: the Tappan Zee (4 km wide), Haverstraw Bay (4.8 km wide), and Newburgh Bay (1.6 km). Summary data on these and other morphometric characteristics are given in Table 1 and Fig. 2.

The Hudson is tidal from New York City to the Federal Green Island Dam (also known as the Troy Dam), located in Troy, NY near the state capital of Albany (242 km from the river mouth). The dam provides an effective barrier to movement of materials upstream of this point, and impedes passage of most estuarine species. The upper, freshwater Hudson is largely controlled through a series of locks and dams, and the New York State Department of Transportation periodically must dredge a 63 km reach of the upriver stretches to maintain a shipping channel.

Salt water enters the Hudson via New York Bay with each tidal flood cycle. Tidal ranges are 1.37 m at the Battery (southern tip of Manhattan), 0.82 m at West Point, and 1.43 m at the head of the estuary at Troy (Darmer 1969). Mean tidal flow averages 12 000 m^3·s^{-1} at the Battery, dropping to zero at Troy. This flux dominates and generally controls the composition of water in the estuary and can exceed the freshwater inflows by 10- to 100-fold (Texas Instruments 1979). Because residence times of water in the estuary are a function of channel volume, morphometry, tidal flux, and freshwater flows, the same parcel of water tends to wash back and forth several times past any given fixed point. Dye studies at Poughkeepsie (km 120) have demonstrated a net (albeit slow) outflow (Hetling et al. 1978). Simpson et al. (1974) estimated flushing time by calculating the ratio of volume to mean annual freshwater flow. This ratio (0.35 yr = 126 days) is smaller than for other large Eastern Seaboard estuaries, indicating relatively more rapid flushing of the system. Also, the shallow depths of the Tappan Zee and Haverstraw Bay tend to function as a sill, limiting saltwater intrusion to the much deeper Hudson Highlands region.

The climate of the Hudson Valley is northern temperate, characterized by distinct seasonal shifts. Annual precipitation averages around 1000 mm (Table 1), most of which occurs in the winter and spring months (NOAA 1982). The pattern of precipitation, particularly the snowmelt and typically heavy spring rains, sends a large seasonal pulse of fresh water and an associated material load into the estuary. Spring runoff is followed by lower freshwater flows during the summer through early fall; lowest flows occur in August. Seasonal intrusion of salt water is greatest at that time, and the salt front, defined as 0.3 μS·cm^{-1}, may reach West Point or Newburgh (80–100 km). Extreme drought conditions can permit saltwater intrusion up to Hyde Park (128 km). The salt front retreats during periods of high freshwater flow to Yonkers (32 km) (Darmer 1969); its time-averaged annual position, computed from Weinstein (1977), is around 60 km from the mouth. Salt and fresh waters mix fairly well in low flow conditions, but distinct, vertical salinity gradients are found under high freshwater flow (Busby and Darmer 1970).

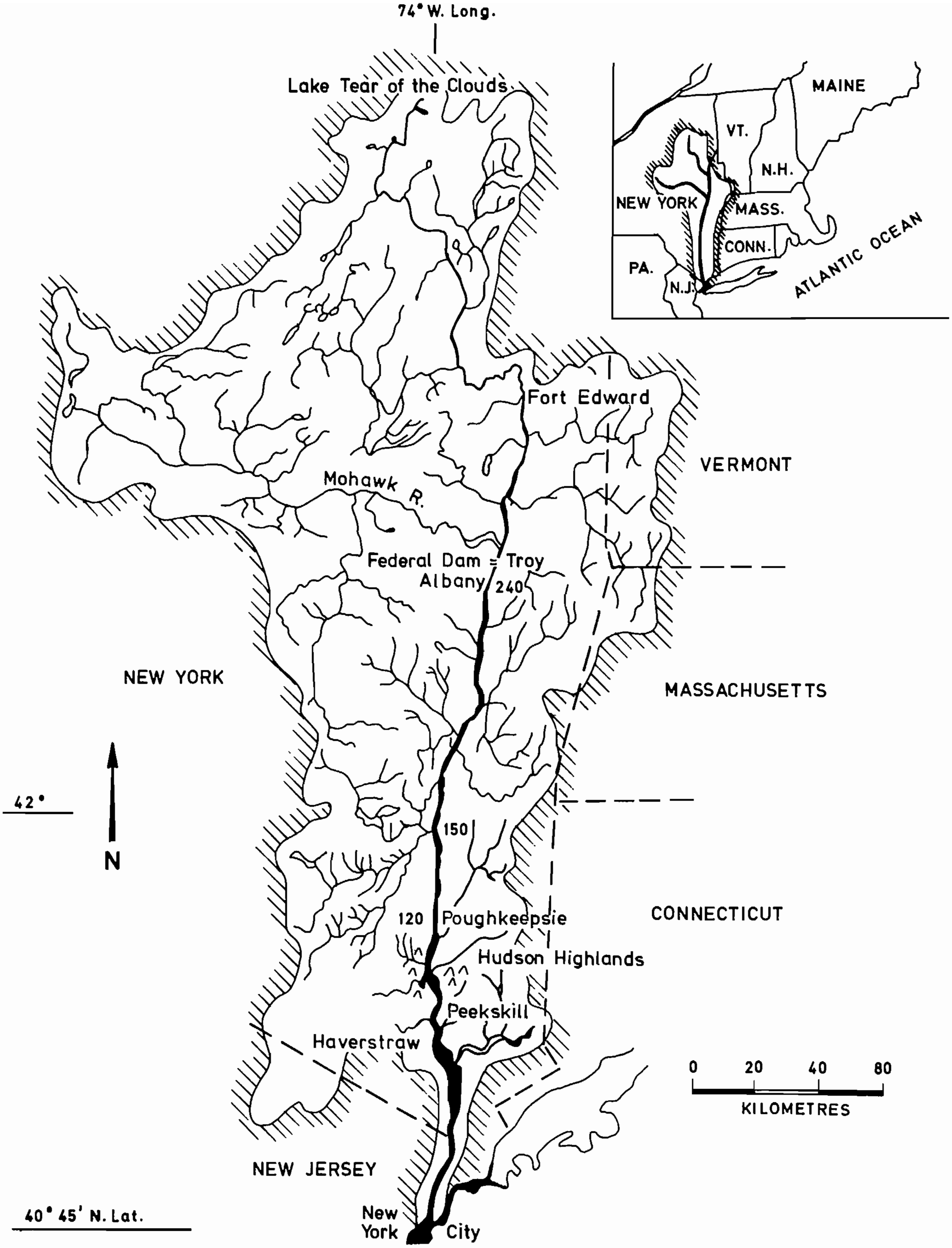


FIG. 1. The Hudson River watershed. River distances (from mouth) marked in kilometres.

TABLE 1. Physical and environmental characteristics of the upper and lower Hudson River.

Parameter	Upper HR	Lower HR	Reference
River Dimensions:			
Length (km)	257	250	—[a]
Avg. width (m)	—	1 280	—[a]
(min.–max.)	—	(260–5 520)	—[a]
Avg. depth (m)	—	10	—[a]
(min.—max.)	—	(4–34)	—[a]
Cross-sectional area (m^2)	—	10 420	—[a]
(min.–max.)		(1 770–21 400)	
Elevation gradient (m•km^{-1})	2.6	0.006	Sanders (1982); Helsinger and Friedman (1982)
River flow (m^3•s^{-1})	392.	623	USGS (1981)
Tidal flow (m^3•s^{-1})	n.a.	5 670–8 500	Busby (1966)
Environment:			
Insolation (kcal•m^{-2}•yr^{-1})	9.6×10^5		SERI (1981)
Avg. temperature (°C):			
Air:	15.3	15.9	NOAA (1982)
Water:	—	12.3	—[b]
Precipitation (mm)	980.	1 140	NOAA (1982)
Drainage area (km^2)	20 917	13 740	Sanders (1982); Helsinger and Friedman (1982)
Allochthonous carbon loading (t•yr^{-1})	66 024	43 431	Gladden et al. (1988)
Anthropogenic Influence:			
Power plants:			
Combined water withdrawal (m^3•yr^{-1})	n.a.	4.66×10^9	Horne (1979)
Avg. within-plants temperature increase (Δ T, °C)	n.a.	8.3	Limburg et al. (1986a)
PCBs:			
Estimated load in sediments (t)	153.2 (including remnant deposits)	78.8	HRF (1984)
Flow over Troy Dam (t•yr^{-1})	0.4 (in 1981)	n.a.	Schroeder and Barnes (1983)
Flow to NY Harbor	n.a.	2.5	Bopp et al. (1981)
Loss to atmosphere (t•yr^{-1})	2.9	—	Tofflemire and Quinn (1979)
Amount in biota (t)	—	—	
Sewage:			
BOD (t•yr^{-1})	1 900	6.8×10^4	Heeling (1976)
Nitrogen (t•yr^{-1})	398	4.0×10^4	Deck (1981)
Phosphorus (t•yr^{-1})	183	0.9×10^4	McFadden et al. (1978)
Dredging: Amount of sediment removed (does not include Westway) (m^3•yr^{-1})	4×10^5	12×10^5	Horne (1979)
Fishing:			
Commercial catch:			
MT•yr^{-1}:	n.a.	mid-1970's: 2 600	—[c]
Value (1000 $):	500		
Recreational catch:			
Angler-days•yr^{-1}:	8–10 000	70 000	—[c]
Estimated value (1000 $):	88–110	770	—[d]

[a] Data sources of estuarine dimensions: Albany to New Hamburg: Stedfast (1982); New Hamburg to the Battery: Darmer (1969) and measurements from 7.5 minute topographic maps.

[b] Calculated with data for ambient monthly water temperatures at Roseton (LMS 1978); Bowline-Lovett (LMS 1977a); upper NY Harbor (Malone 1977).

[c] Sheppard (1983) developed rough estimates of the contribution of the Hudson River to various fisheries, including some marine fisheries.

[d] Assumes that a conservative estimate for an angler-day value is $11.00 (New York State Economic Development Board 1975).

n.a. = not applicable.

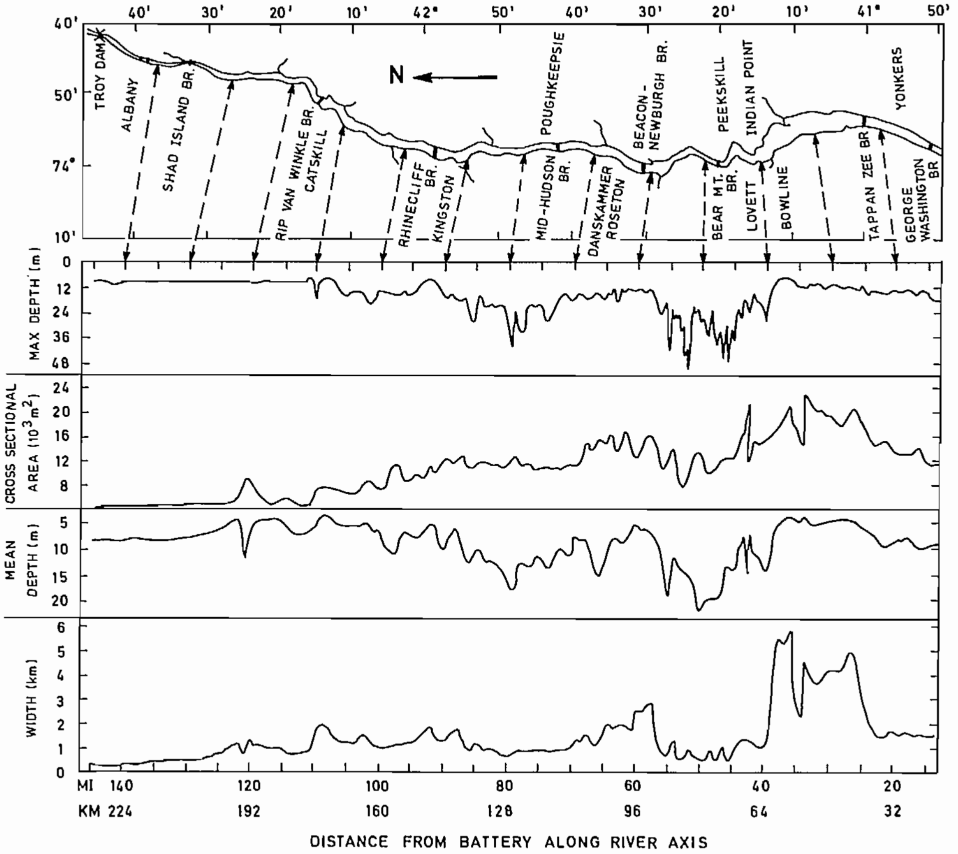


FIG. 2. Maximum depth, cross sectional area, mean depth, and width of the Hudson River estuary (redrawn from Klauda et al. 1981).

Roughly 80% of the estuary's fresh water derives from above the Troy Dam (notably from the Mohawk River, the largest tributary). Most of the remainder enters from smaller, upper-estuary tributaries (McFadden et al. 1977). Freshwater flows at the U.S. Geological Survey's gauging station at Green Island average 392 $m^3 \cdot s^{-1}$ (USGS 1981), corresponding to an estimated flow of 538–567 $m^3 \cdot s^{-1}$ in the estuary proper (Central Hudson Gas and Electric 1977). Time-series analysis of river discharge by Apicella and Zimmie (1978) revealed a strong 20-yr periodicity in freshwater flow rates. At present, the Hudson Valley appears to be nearing the end of a drought phase, much as it did 20 years ago.

Water Quality

Temperature, salinity, and dissolved oxygen vary up and down the length of the river, as do levels of pollutants and other transported materials.

Dissolved oxygen (DO) values reach maximum levels in late winter/early spring, when the water is coldest. Levels of DO typically drop in the estuary in the summer, particularly in areas where biochemical oxygen demand (BOD) from sewage loading is high (metropolitan New York area). Although DO values have been monitored more-or-less routinely in parts of the estuary since the early 1970's, relatively few interannual comparisons of levels have been made. Figure 3 shows profiles of dissolved oxygen, corrected for temperature and salinity, expressed as a percent of O_2 saturation (calculated with data from Texas Instruments 1979; Abood et al. 1976; Fleming et al. 1976; USGS 1969). As can be seen in Figure 3b, DO levels have improved since the implementation of the 1972 amendments of the Federal Water Pollution Control Act ("Clean Water Act") in the mid-1970's, particularly between the cities of Albany (km 240) and Kingston (km 160).

Allochthonous organic matter, including major nutrients, enters the river via tributaries and human point sources. Figure 4, taken from a study by Gladden et al. (1988), indicates that upriver loading of carbon is correlated with water discharge. High-runoff events following snowmelt carry most of the organic matter to the estuary, but the material tends to flush through rather than remain in the system. Upper watershed loadings are estimated to account for 66 024 t carbon annually, or roughly 27% of all inputs; lower watershed and sewage (mainly New York City environs) to account for 43 254 t (18%) and 57 649 t (23.5%), respectively (Limburg et al. 1986a). Exclusion of the metropolitan New York influence results in considerably lower estimates for carbon loadings to the Hudson below Troy (R.W. Howarth, Cornell University, pers. comm.).

At the river's mouth, discharges of wastewater from the metropolitan New York and New Jersey areas amount to roughly 16.3 × 10^6 $m^3 \cdot d^{-1}$ (Brosnan et al. 1987). New York City itself processes about half of this amount through 14 water pollution control plants, 9 of which provide full secondary treatment. The City of New York Department of Environmental Protection has maintained a water quality

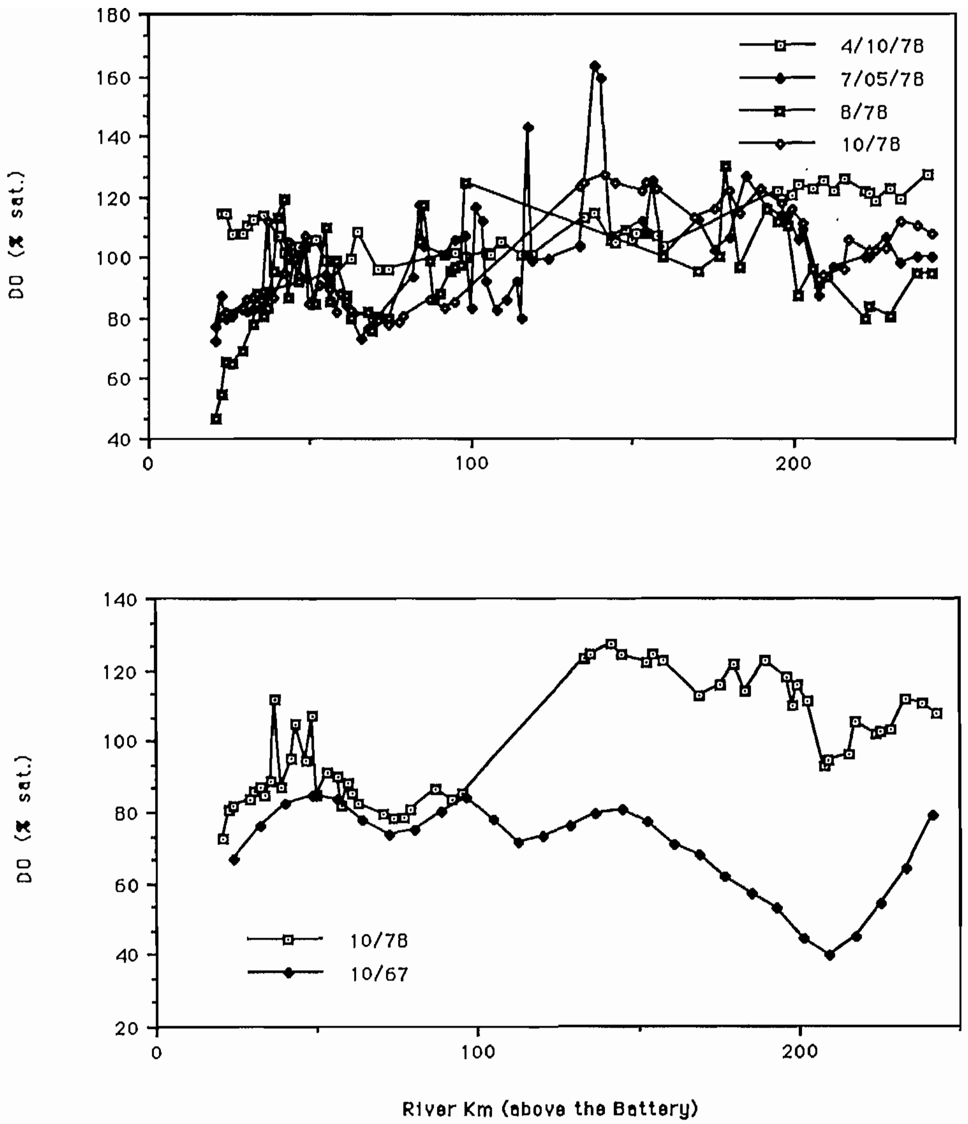


FIG. 3. Hudson River dissolved oxygen (DO) profiles, expressed as percentages of DO in saturated water. (a) Profiles for April, July, August, and October, 1978. (b) Profiles comparing October, 1967 with October, 1978. (Source: Limburg et al. 1986a).

monitoring program since 1909; improvements in dissolved oxygen and coliform counts were seen to correspond to online entry of new sewage treatment plants, although heavy metal (except for lead) and phosphorus removal efforts have not been as successful (Brosnan et al. 1987). Much of the metallic and nutrient load is carried through 8400+ km of combined sewers that carry industrial and domestic wastes together with surface runoff (Brosnan et al. 1987).

Inputs of nitrogen and phosphorus (N and P) are dominated strongly by sewage loadings from urbanized areas. About 83% of P inputs and 70% of N enter the Hudson between the Tappan Zee Bridge (km 40) and Upper New York Bay (Deck 1981). Most of the nitrogen enters as NH_4-N in sewage and runoff (Fig. 5) (Deck 1981). In-river algal uptake of nutrients is small relative to the amount available in the reaches below the Tappan Zee Bridge (Garside et al. 1976; Malone 1977); this trend changes in the middle reaches of the Hudson between approximately Kingston and Poughkeepsie where experiments suggest some phosphorus limitation in addition to light limitation (R.W. Howarth, Cornell University, pers. comm.). Much of the dissolved N is transported to the New York Bight, where it is gradually assimilated by nanno-phytoplankton in the plume of the estuary (Malone 1977, 1984).

The Food Web and Energy Flow

The trophic organization of the Hudson is typical of most estuaries, with a mix of resident and migratory species that follow the salinity gradient (Ristich 1977; Woodhead 1987). What may be atypical, however, is the predominance of exogenous sources of carbon (i.e., fixed energy) over endogenous ones. Direct total production by phytoplankton and macrophytes amounts to only 17% of all organic carbon inputs to the estuary, whereas watershed inputs account for 44%, and sewage for another 24% (Table 2). The precise fate of all the incoming sources of energy is far from clear. Much of the allochthonous material enters the food web

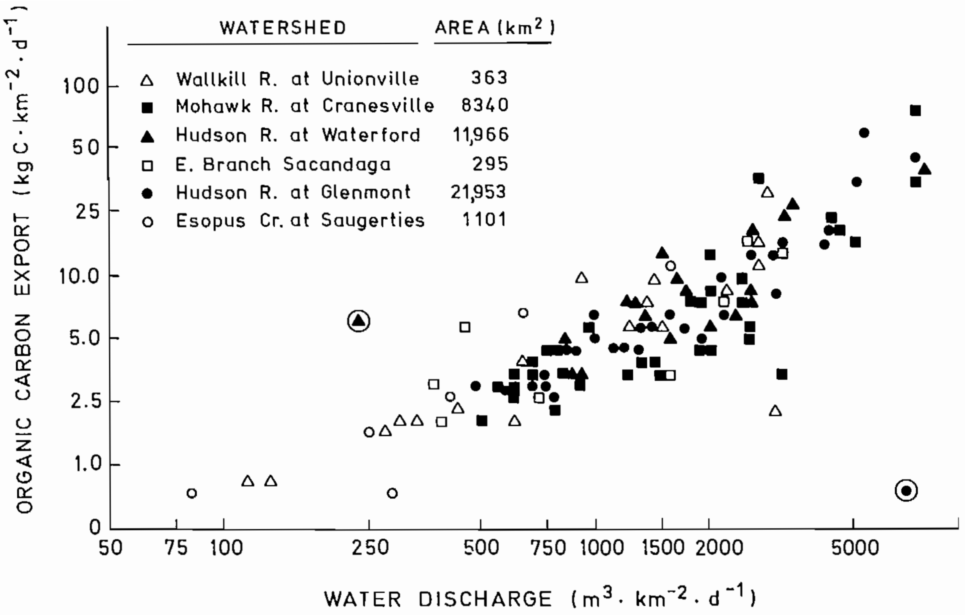


FIG. 4. Plot of freshwater discharge (m^3• km^{-2}• d^{-1}) from various tributaries in the Hudson watershed vs. transport rates of organic carbon exported from the tributary watersheds (kg C• km^{-2}• d^{-1}). (Source: Gladden et al. 1988)

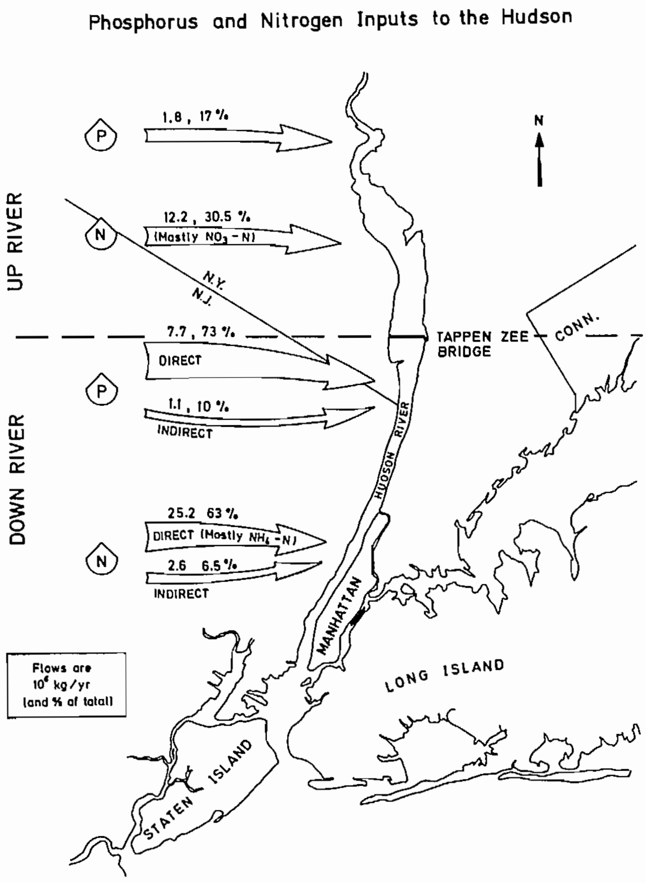


FIG. 5. Phospate and nitrogenous inputs to the Hudson estuary.

through benthic and microbiological pathways. Autochthonous materials pass through both pelagic and benthic organisms.

Much of the Hudson's primary production is accounted

TABLE 2. Organic carbon inputs to the Hudson River estuary (Limburg et al. 1986a).

Source	Carbon t•yr^{-1}	Percent of total
Phytoplankton	36 364[a]	14.8
Macrophytes:		
Emergent	3 936[b]	1.6
Tidal Flats	1 428[c]	0.6
Upper Watershed (Above km 245)	66 024[d]	26.8
Lower Watershed (km 0–245)	43 254[e]	17.6
Sewage (km 0–245)	57 649[f]	23.5
Marine	36 898[g]	15.0
Total	245 553	100

[a] Estimated semi-annual (May–October) primary productivity (Sirois and Frederick 1978), increased by 5 % to cover the remaining months of the year.

[b] Emergent marsh area estimated at 9.6 km^2; net annual production assumed to be 1000 g•m^{-2}•yr^{-1}; energy content of biomass assumed to be 4.1 kcal•g^{-1} dry weight (McFadden et al. 1978); carbon equivalents assumed to be 1 g C per 10 kcal (Odum 1971).

[c] Tidal flat area estimated at 10.2 km^2; annual production assumed to be 140 g•m^{-2}•yr^{-1} (Cadee and Hegeman 1974; Marshall et al. 1971).

[d] From Gladden et al., (1988). (8.633 kg•km^{-2}•day^{-1}; upper watershed area = 20 953 km^2.

[e] Lower watershed area = 13 727 km^2.

[f] Municipal and industrial BOD discharges 217.4 t•day^{-1} (Hetling 1976; McFadden et al. 1978); 0.7265 kg C per kg BOD.

[g] Phytoplankton from marine sources (winter through summer) estimated at 6 200 t C annually (Malone et al. 1980). Sewage input from the New York Bight assumed to be 30 680 t C•yr^{-1} (McFadden et al. 1978).

for by phytoplankton and submersed macrophyte beds, with plants from emergent and tidal flat areas comprising the remainder. Peak production occurs in the broad, lower estuarine bays (Tappan Zee and Haverstraw Bay) as well as in New York Bay just beyond the mouth of the estuary. In 1972, maximum production values exceeded 5.5 g C•m^{-2}•d^{-1} in June and July (Sirois and Frederick 1978); upriver production in the Poughkeepsie–Kingston reach is considerably lower (J. Cole, Inst. of Ecosystem Studies, pers. comm.). Production generally is thought to be light-limited rather than constrained by nutrients (Gladden et al. 1988), although this relationship is weaker in the freshwater reaches than it is in the metropolitain New York vicinity, where phosphorus can have a limiting effect in late summer (R. Howarth, Cornell University, pers. comm.). In the lower estuary, high turbidities restrict most available light to the top meter of the water column (NYU 1978), whereas nutrient inputs are nearly always in excess of plant uptake requirements (Hetling 1976; Malone 1977). The annual cycle of planktonic production begins with a spring bloom of diatoms, followed in mid-summer by a shift to green algae, dominated by nannoplankton, and blue-green algae that are seen in warm summer months (Heffner 1973; McFadden et al. 1978; Weinstein 1977). In fall and winter, production drops to <0.1 g C•m^{-2}•d^{-1} (Gladden et al. 1988) and is attributed to diatoms.

Secondary production proceeds through both pelagic and benthic pathways; the annual ranges of production appear to be greater for zooplankton than for benthic organisms (30-fold (Malone 1977) to 100-fold (NYU 1976) ranges in copepod larval abundances vs. three-fold changes in benthic invertebrate populations (Texas Instruments 1976)). Such data as exist indicate considerable variability in terms of biomass, production, and respiration (Table 3). Dominant zooplankton species include microcrustaceans such as *Eurytemora affinis, Bosmina longirostris,* and *Acartia tonsa*, which are important sources of food for larval striped bass, white perch, Atlantic tomcod, herring, and other young fish. Representative important benthic species include annelids such as *Scolecolepides*, crustaceans such as *Crangon*, *Palaemonetes*, and *Gammarus*, as well as various gastropods (e.g., *Hydrobia*), oligochaetes, and chironomid larvae (Ristich et al., 1977).

Despite its popular reputation as a ''dead'' river, the Hudson actually supports at least 184 species of fish from 65 different families (Brandt 1981; C.L. Smith, American Museum of Natural History, pers. comm.), including several species of commercial and recreational importance such as striped bass, bluefish, white perch, black bass, American shad, American eel, and Atlantic sturgeon (Table 4). Since the construction of the Federal Dam at Troy in 1826, the upper Hudson has been cut off biologically from the lower river, at least for many anadromous species that formerly spawned in the upper reaches. Blueback herring are a notable exception, ascending the Mohawk River as far west as Utica and beyond. At least some American shad and striped bass have been captured above the Troy Dam as well. In response to improved water quality in the upper estuary, fish stocks are increasing in that reach; additional passage of fish into the upper Hudson can be anticipated.

Most species that have been monitored appear to have stable or even increasing populations over the last decade (A. Kahnle, NY State Dept. of Environmental Conservation, pers. comm.). This finding is in sharp contrast to the decline in many major stocks of commercially important fish in other U.S. east coast estuaries, particularly the Chesapeake Bay. Figure 6, from the Emergency Striped Bass Research Study (FWS 1985), shows time series of indexes of striped bass juvenile abundance for several Atlantic coast estuaries; the Hudson is the only region in which stocks did not decline severely from the mid-1970's.

Stock assessment techniques that have been used over the years have produced relative measures of abundances, such as catch-per-effort statistics; also, during the period of power plant impact assessments, mark–recapture studies of striped bass, white perch, and Atlantic tomcod provided abundance estimates for different river reaches (Texas Instruments 1981). Beach seines and off-shore trawls have been conducted both experimentally during impact assessment of power plants and as part of monitoring programs carried out by the New York State Department of Environmental Conservation (DEC). Figure 7 is a chart of the most abundant species caught in a beach seine program in the late summer/early fall of 1981 (Kahnle and Brandt 1985). There, blueback herring, white perch, American shad, and banded killifish accounted for 42, 22, 7, and 7 % of the total catch, respectively; bay anchovy, white perch, and hogchoker accounted for 80–88 % of total catches in bottom trawl collections from 1981 to 1984 (Kahnle and Brandt

TABLE 3. Annual flows and storages in the lower Hudson River estuary (km −16 to 106) (Limburg et al. 1986a).

Parameter	Lower[a] NY Bay	Upper[b] NY Bay	Tappan Zee	Bowline[c] Point	Indian[d] Point	Roseton-[e] Danskammer
Primary Productivity (g C•m^{-2}•yr^{-2})	800	200	250[f]	170	290	200
Phytoplankton Biomass (g C•m^{-2})	n.a.	n.a.	n.a.	0.01	n.a.	0.5–2.4
Chlorophyll-*a* (μg•L^{-1})	10.4	2.62	26.4[f]	9.92	2.1	5.6
Nutrients:						
N (mg•L^{-1})	0.43	0.71	n.a.	0.88	n.a.	0.77
PO_4-P (mg•L^{-1})	0.05	0.09	n.a.	0.05	n.a.	0.04
Si (mg•L^{-1})	0.32	n.a.	n.a.	2.4	n.a.	n.a.
Zooplankton (g wet wt•m^{-3})	n.a.	0.01–0.3	n.a.	0.014	0.031	n.a.
Benthic Fauna (g wet wt•m^{-2})	4.07–804[h]	n.a.	n.a.	2.91(1975) 24.8(2974)	16.2(1973) 31.0(1974)	6.89–19.8
Benthic Respiration (g C•m^{-2}•yr^{-1})	126–1018[h]	n.a.	n.a.	407–1347[g]	n.a.	n.a.

[a] Data from O'Reilly et al. (1976) unless otherwise specified.
[b] Data from Malone (1977) unless otherwise specified.
[c] Data from EA (1981), LMS (1977a, 1980).
[d] Data from NYU (1974), TI (1974, 1975).
[e] Data from LMS (1977b, 1981).
[f] Sirois and Fredrick (1978).
[g] Thomas et al. (1976).
[h] Pearce et al. (1981).
n.a. = not available

TABLE 4. Fish species in the Hudson River.

Family and Common Name[a]	Scientific Name	Occurence[b]
Petromyzontidae — Lampreys		
Silver lamprey	*Ichthyomzon unicuspis*	A
American brook lamprey	*Lampetra appendix*	A
Sea lamprey	*Petromyzon marinus*	A
Carcharhinidae — Requiem Sharks		
Dusky shark	*Carcharhinus sp.*	S
Rajidae — Skates		
Barndoor skate	*Raja laevis*	S
Acipenseridae — Sturgeons		
Shortnose sturgeon[c]	*Acipenser brevirostrum*	A
Atlantic sturgeon	*Acipenser oxyrhynchus*	A
Amiidae — Bowfins		
Bowfin	*Amia calva*	F
Elopidae — Tarpons		
Ladyfish	*Elops saurus*	S
Anguillidae — Freshwater eels		
American eel	*Anguilla rostrata*	A
Congridae — Conger eels		
Conger eel	*Conger oceanicus*	S
Clupeidae — Herrings		
Blueback herring	*Alosa aestivalis*	A
Hickory shad	*Alosa mediocris*	S
Alewife	*Alosa pseudoharengus*	A
American shad	*Alosa sapidissima*	A
Atlantic menhaden	*Brevoortia tyrannus*	A
Atlantic herring	*Clupea harengus harengus*	S
Gizzard shad	*Dorosoma cepedianum*	A
Round herring	*Etrumeus teres*	S
Engraulidae — Anchovies		
Striped anchovy	*Anchoa hepsetus*	S

TABLE 4. (*Continued*)

Family and Common Name[a]	Scientific Name	Occurence[b]
Bay anchovy	*Anchoa mitchilli*	S
Synodontidae — Lizardfishes		
Inshore lizardfish	*Synodus foetens*	A
Ictaluridae — Freshwater catfishes		
White catfish	*Ictalurus catus*	F
Yellow bullhead	*Ictalurus natalis*	F
Brown bullhead	*Ictalurus nebulosus*	F
Channel catfish	*Ictalurus punctatus*	F
Stonecat	*Noturus flavus*	O/F
Tadpole madtom	*Noturus gyrinus*	O/F
Margined madtom	*Noturus insignis*	O/F
Catostomidae — Suckers		
Longnose sucker	*Catostomus catostomus*	F
White sucker	*Catostomus commersoni*	F
Creek chubsucker	*Erimyzon oblongus*	O/F
Northern hog sucker	*Hypentelium nigricans*	F
Shorthead redhorse	*Moxostoma macrolepidotum*	F
Cyprinidae — Minnows and Carps		
Goldfish	*Carassius auratus*	F/I
Redside dace	*Clinostomus elongatus*	F
Lake chub	*Couesius plumbeus*	F
Common carp	*Cyprinus carpio*	F/I
Cutlips minnow	*Exoglossum maxillingua*	F
Brassy minnow	*Hybognathus hankinsoni*	F
Eastern silvery minnow	*Hybognathus regius*	F
Hornyhead chub	*Nocomis biguttatus*	F
Golden shiner	*Notemigonus crysoleucas*	F
Comely shiner	*Notropis amoenus*	F
Satinfin shiner	*Notropis analostanus*	F
Emerald shiner	*Notropis atherinoides*	F
Bridle shiner	*Notropis bifrenatus*	F
Ironcolor shiner	*Notropis chalybaeus*	F
Common shiner	*Notropis cornutus*	F
Blackchin shiner	*Notropis heterodon*	F
Blacknose shiner	*Notropis heterolepis*	F
Spottail shiner	*Notropis hudsonius*	F
Rosyface shiner	*Notropis rubellus*	F
Spotfin shiner	*Notropis spilopterus*	F
Sand shiner	*Notropis stramineus*	F
Mimic shiner	*Notropis volucellus*	F
Northern redbelly dace	*Phoxinus eos*	F
Finescale dace	*Phoxinus neogaeus*	F
Bluntnose minnow	*Pimephales notatus*	F
Fathead minnow	*Pimephales promelas*	F
Blacknose dace	*Rhinichthys atratulus*	F
Longnose dace	*Rhinichthys cataractae*	F
Bitterling	*Rhodeus sericeus*	F
Rudd	*Scardinius erythrophthalmus*	F/I
Creek chub	*Semotilus atromaculatus*	F/I
Fallfish	*Semotilus corporalis*	F
Pearl dace	*Semotilus margarita*	F
Salmonidae — Trouts		
Cisco or lake herring	*Coregonus artedii*	O/F
Lake whitefish	*Coregonus clupeaformis*	O/F
Round whitefish	*Prosopium cylindraceum*	O/F
Sockeye salmon	*Oncorhynchus nerka*	A
Atlantie salmon	*Salmo salar*	A
Rainbow trout	*Salmo gairdneri*	O/F
Brown trout	*Salmo trutta*	A
Brook trout	*Salvelinus fontinalis*	O/F
Lake trout	*Salvelinus namaycush*	O/F
Osmeridae — Smelts		
Rainbow smelt	*Osmerus mordax*	A
Umbridae — Mudminnows		

TABLE 4. (*Continued.*)

Family and Common Name[a]	Scientific Name	Occurence[b]
Central mudminnow	*Umbra limi*	F
Eastern mudminnow	*Umbra pygmaea*	F
Esocidae — Pikes		
Redfin pickerel	*Esox americanus*	F
Northern pike	*Esox lucius*	F
Chain pickerel	*Esox niger*	F
Percopsidae — Trout-perches		
Trout-perch	*Percopsis omiscomaycus*	F
Lophiidae — Goosefishes		
Goosefish	*Lophius americanus*	S
Batrachoididae — Toadfishes		
Oyster toadfish	*Opsanus tau*	S
Gadidae — Codfishes		
Fourbeard rockling	*Enchelyopus cimbrius*	S
Atlantic cod	*Gadus morhua*	S
Silver hake	*Merluccius bilinearis*	S
Atlantic tomcod	*Microgadus tomcod*	S
Pollock	*Pollachius virens*	S
Red hake	*Urophycis chuss*	S
Spotted hake	*Urophycis regia*	S
Ophidiidae — Cusk Eels		
Striped cusk eel	*Ophidion marginatum*	S
Belonidae — Needlefishes		
Atlantic needlefish	*Strongylura marina*	S
Cyprinodontidae — Killifishes		
Sheepshead minnow	*Cyprinodon variegatus*	A
Banded killifish	*Fundulus diaphanus*	F
Mummichog	*Fundulus heteroclitus*	A
Striped killifish	*Fundulus majalis*	S
Atherinidae — Silversides		
Reef silverside	*Hypoatherina harringtonensis*	S
Brook silverside	*Labidesthes sicculus*	O/F
Rough silverside	*Membras martinica*	S
Inland silverside	*Menidia beryllina*	S
Atlantic silverside	*Menidia menidis*	S
Gasterosteidae — Sticklebacks		
Fourspine stickleback	*Apeltes quadracus*	A
Brook stickleback	*Culaea inconstans*	O/F
Threespine stickleback	*Gasterosteus aculeatus*	A
Ninespine stickleback	*Pungitius pungitius*	O/F
Fistulariidae — Cornetfishes		
Bluespotted cornetfish	*Fistularia tabacaria*	S
Syngnathidae — Pipefishes		
Lined seahorse	*Hippocampus erectus*	S
Northern pipefish	*Syngnathus fuscus*	S
Moronidae — Temperate basses		
White perch	*Morone americana*	A
White bass	*Morone chrysops*	A
Striped bass	*Morone saxatilis*	A
Serranidae — Seabasses		
Black sea bass	*Centropristis striata*	S
Centrarchidae — Sunfishes		
Mud sunfish	*Acantharchus pomotis*	F
Rock bass	*Ambloplites rupestris*	F
Bluespotted sunfish	*Enneacanthus gloriosus*	F
Banded sunfish	*Enneacanthus obesus*	F
Redbreast sunfish	*Lepomis auritus*	F
Green sunfish	*Lepomis cyanellus*	O/F
Pumpkinseed	*Lepomis gibbosus*	F
Warmouth	*Lepomis gulosus*	F
Bluegill	*Lepomis macrochirus*	F
Smallmouth bass	*Micropterus dolomieui*	F
Largemouth bass	*Micropterus salmoides*	F
White crappie	*Pomoxis annularis*	F

TABLE 4. (*Continued.*)

Family and Common Name[a]	Scientific Name	Occurence[b]
Black crappie	*Pomoxis nigromaculatus*	F
Percidae — Perches		
Greenside darter	*Etheostoma blennioides*	F
Fantail darter	*Etheostoma flabellare*	F
Tessellated darter	*Etheostoma olmstedi*	F
Yellow perch	*Perca flavescens*	F
Logperch	*Percina caprodes*	F
Shield darter	*Percina peltata*	F
Walleye	*Stizostedion vitreum vitreum*	F
Priacanthidae — Bigeyes		
Short bigeye	*Pristigenys alta*	S
Pomatomidae — Bluefishes		
Bluefish	*Pomatomus saltatrix*	S
Rachycentridae — Cobias		
Cobia	*Rachycentron canadum*	S
Carangidae — Jacks and pompanos		
Crevalle jack	*Caranx hippos*	S
Atlantic moonfish	*Selene setapinnis*	S
Lookdown	*Selene vomer*	S
Echeneididae — Remoras		
Sharksucker	*Echeneis naucrates*	S
Lutjanidae — Snappers		
Gray snapper	*Lutjanus griseus*	S
Gerridae — Mojarras		
Spotfin mojarra	*Eucinostomus argenteus*	S
Haemulidae — Grunts		
Pigfish	*Orthopristis chrysoptera*	S
Sparidae — Porgies		
Pinfish	*Lagodom rhomboides*	S
Scup	*Stenotomus chrysops*	S
Sciaenidae — Croakers		
Silver perch	*Bairdiella chrysoura*	S
Weakfish	*Cynoscion repalis*	S
Spot	*Leiostomus xanthurus*	S
Northern kingfish	*Menticirrhus saxatilis*	S
Atlantic croaker	*Micropogonias undulatus*	S
Labridae — Wrasses		
Tautog	*Tautoga onitis*	S
Cunner	*Tautogolabrus adspersus*	S
Mugilidae — Mullets		
Striped mullet	*Mugil cephalus*	S
White mullet	*Mugil curema*	S
Sphyraenidae — Barracudas		
Guaguanache	*Sphyraena guachancho*	S
Uranoscopidae — Stargazers		
Northern stargazer	*Astroscopus guttatus*	S
Blennidae — Blennies		
Freckled blenny	*Hypsoblennius ionthus*	S
Pholidae — Gurmels		
Rock gurmel	*Pholis gunellus*	S
Ammodytidae — Sandlances		
American sandlance	*Ammodytes americanus*	S
Eleotridae—Sleepers		
Fat sleeper	*Dormitator maculatus*	A
Gobiidae—Gobies		
Naked goby	*Gobiosoma bosci*	S
Seaboard goby	*Gobiosoma ginsburgi*	S
Trichiuridae — Cutlassfishes		
Atlantic cutlassfish	*Trichiurus lepturus*	S
Scombridae—Mackerels and tunas		
Atlantic mackerel	*Scomber scombrus*	S
Stromateidae-Butterfishes		
Butterfish	*Peprilus triacanthus*	S
Triglidae—Searobins		

TABLE 4. (*Concluded.*)

Family and Common Name[a]	Scientific Name	Occurence[b]
Northern searobin	*Prionotus carolinus*	S
Striped searobin	*Prionotus evolans*	S
Cottidae—Sculpins		
Slimy sculpin	*Cottus cognatus*	O/F
Grubby	*Myoxocephalus aenaeus*	F
Longhorn sculpin	*Myoxocephalus octodecemspinosus*	S
Cyclopteridae — Snailfishes		
Seasnail	*Liparis atlanticus*	S
Dactylopteridae		
Flying gurnard	*Dactylopterus volitans*	S
Bothidae—Lefteye flounders		
Gulf Stream flounder	*Citharichthys arctifrons*	S
Smallmouth flounder	*Etropus microstomus*	S
Summer flounder	*Paralichthys dentatus*	S
Fourspot flounder	*Paralichthys oblongus*	S
Windowpane	*Scophthalmus aquosus*	S
Pleuronectidae—Righteye flounders		
Yellowtail flounder	*Limanda ferruginea americanus*	S
Winter flounder	*Pseudopleuronectes americanus*	S
Soleidae—Soles		
Hogchoker	*Trinectes maculatus*	S
Balistidae—Leatherjackets		
Orange filefish	*Aluterus schoepfi*	S
Tetraodontidae—Puffers		
Northern puffer	*Sphoeroides maculatus*	S
Diodontidae — Porcupinefishes		
Striped burrfish	*Chilomycterus schoepfi*	S
Total families	65	
Total species		184

[a] Family order follows Lauder and Liem (1983).

[b] Definition of occurence: O — Inhabitant of other than the Hudson River Estuary, A — Inhabits both salt water and fresh during life cyle, F — Inhabits fresh water during entire life cycle, S — Inhabits salt water during entire life cycle, I — Introduced species.

[c] Endangered species.

1985). Striped bass abundances were ~5% for bottom trawls and beach seine studies.

Figure 8 shows temporal and spatial variation in egg distributions for six major fish species in 1974 (data assembled by Boreman 1981). Variation within species can be as great from one year to the next as within-year. Boreman (1981), Gladden et al. (1988), and others (cf. Crecco and Savoy 1985 for shad in the Connecticut River) attribute some of the variability to differences in temperature and freshwater outflow at critical life periods (e.g., egg, yolksac, and postyolksac larval stages). For some of the closely related species, such as the clupeids and *Morone* spp., spatio-temporal segregation may help to reduce interspecific competition for food, as suggested by Schmidt et al. (1988) in a study of early life stages of blueback herring, alewife, and American shad.

Although quantification of biomass has been difficult, a picture emerges of the food web of the Hudson River as a cascade of processes and interactions, beginning with the returning sun that warms the system, drives snowmelt and runoff, brings spring rains, and precipitates a burst of primary and secondary production.

Fisheries Exploitation

Since prehistoric times, the Hudson has supported a mix of subsistence, commercial, and recreational fisheries. In the last century, substantial fisheries have existed for American shad, striped bass, Atlantic and shortnose sturgeon, American eel, alewife, blueback herring, white perch, white catfish, rainbow smelt, and goldfish (Brandt 1981). Overfishing of certain species, particularly American shad and sturgeon, was evident at the turn of the century (Sheppard 1976).

A comprehensive survey of the biological resources (emphasizing fish) of the Hudson was conducted in 1932 (upper watershed) and 1936 (lower watershed) by the New York State Conservation Department (NYS Conservation Dept. 1933, 1937). The most complete, recent evaluation of the Hudson's fisheries resources was made by Sheppard (1976, 1983). In his historical review, Sheppard noted that many anadromous fish species utilized the upper portions of the river prior to the construction of the Federal Dam at Troy.

Commercial — Although good records were not kept until ca. 1880, fisheries were long established for American shad, American eel, Atlantic tomcod, and both Atlantic and shortnose sturgeon. Nineteenth-century sturgeon markets in Albany sold their product as "Albany beef" because of ample supply and large demand (Moore 1937). Shellfish, primarily oysters, also were harvested in the lower estuary where their range extended into Haverstraw Bay, and con-

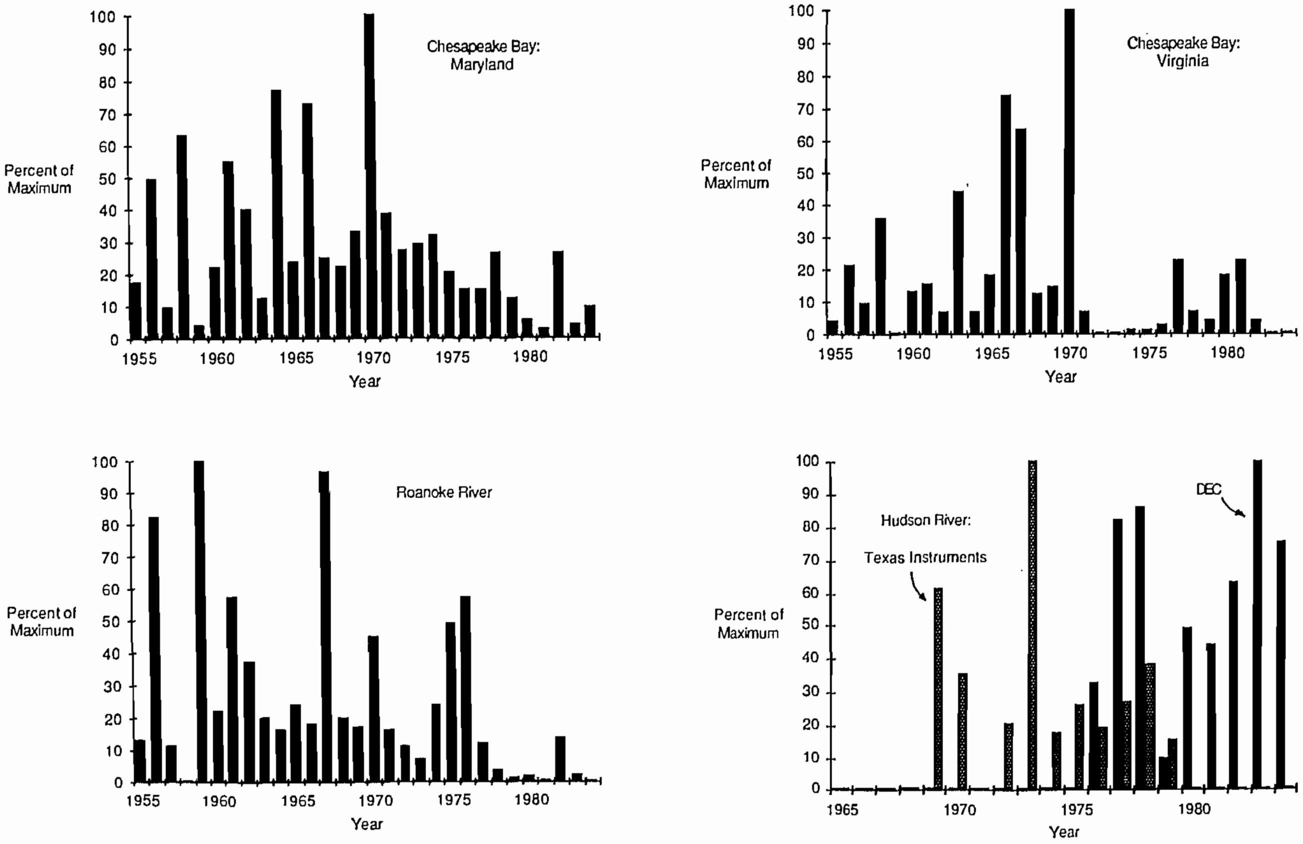
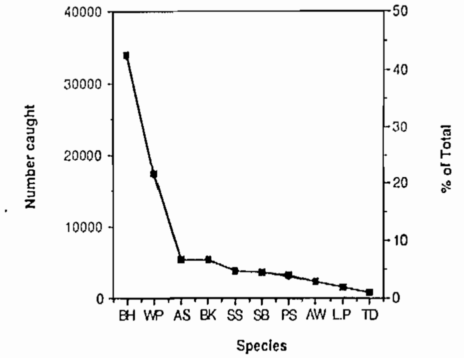


FIG. 6. Comparison of juvenile abundance indexes for striped bass from several East Coast estuaries.



Key: BH - blueback herring; WP - white perch; AS - American shad; BK- banded killifish; SS - spottail shiner; SB - striped bass; PS - pumpkinseed; AW - alewife; LP - Lepomis spp.; TD - tesselated darter.

FIG. 7. Ten most abundant species taken in beach seine hauls, 1981.

stituted a multi-millon dollar industry until pollution forced this fishery to close in 1925 (Sheppard 1976).

American shad has provided the only stable, large-scale commercial fishery throughout the last century, with catches ranging from 18.3 to 1732 t•yr^{-1} (Sheppard 1976). There appear to have been two major periods of high catches in this fishery (Fig. 9). The causes for the fluctuations are unexplained, except that the declines following large catches have been attributed to overfishing (Talbot 1954; Klauda et al. 1977). Other data that may have shed some light on the swings, such as age structure of the shad population, predation factors, and productivity indices, are unavailable.

In the twentieth century, overall commercial landings of fish peaked in the 1930's and 1940's. The largest reported commercial catch occurred in 1945 and amounted to 1060.4 t (89% of which was American shad), valued at $214,194 (Sheppard 1976). Because of a general drop in shad catches throughout the Atlantic Seaboard states, the U.S. Fish and Wildlife Service, in cooperation with state agencies, began a 6-yr investigation into possible causes of the decline (Talbot 1954). A number of factors were examined, including fishing effort, pollution (sewage), dredging, water temperatures, and shipping traffic; of these, fishing effort was seen as having the greatest influence on estimated abundances (Talbot 1954; Burdick 1954). The decline in catches continued into the 1960's and 1970's; abundance indices showed an oscillating, yet generally declining trend from 1931 to 1975 (Klauda et al. 1977). Effort dropped accordingly from a maximum of 95 full-time fishermen in 1945 to only 6 in 1964 (Sheppard 1976). Other indexes of effort (e.g., number of vessels and lengths of various kinds of deployed gear) showed similar declines. Costs of vessels and equipment exceeded the demand for fish products, forcing many fishermen to go out of business or to take on other part-time employment. There is some indication that the stock decline was precipitated by overfishing attributable to changes to more efficient gear types (Sheppard 1976).

Until 1976, striped bass was of some commercial impor-

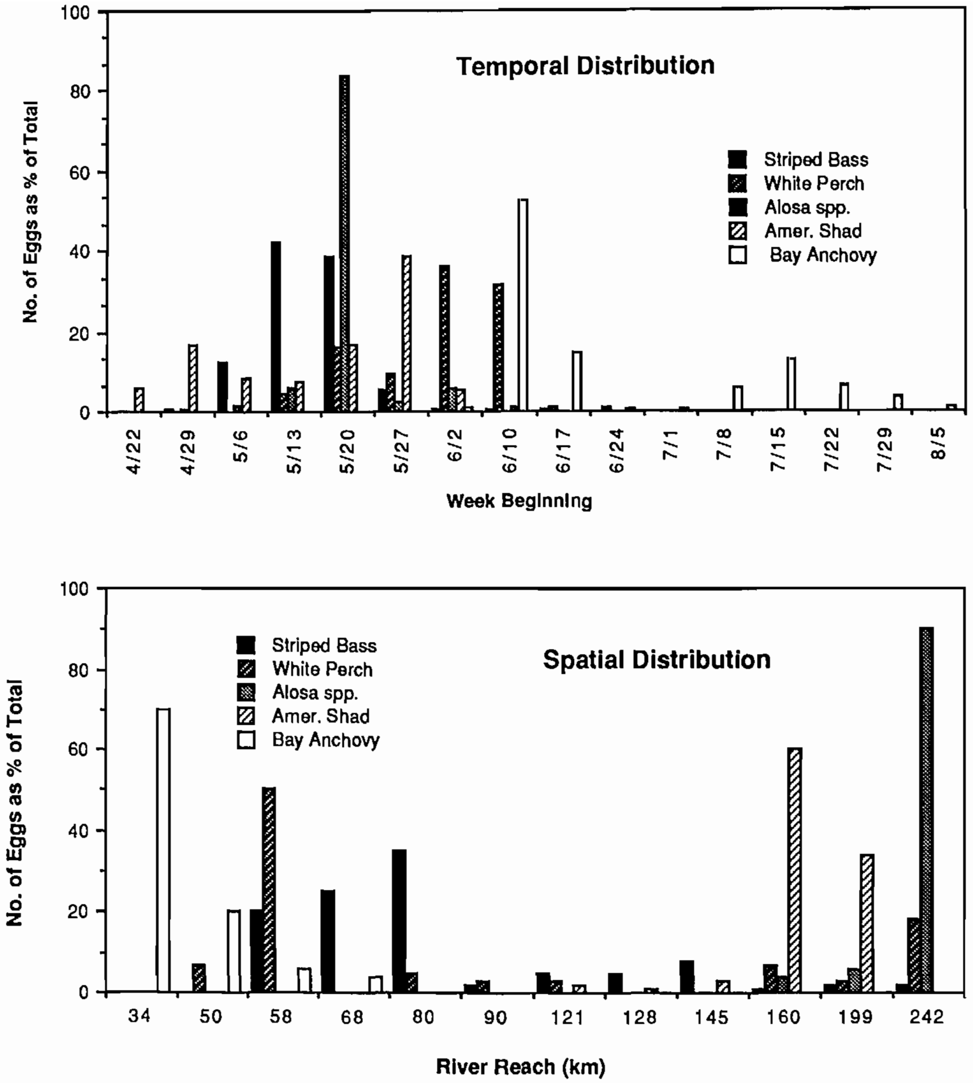


FIG. 8. Egg distributions for six Hudson River fish, 1974. (a) Temporal, (b) Spatial.

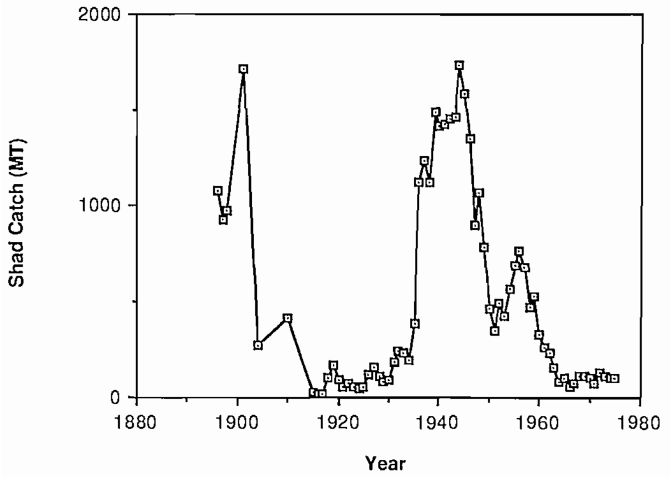


FIG. 9. Catches of American shad (*Alosa sapidissima*) in the Hudson River, 1896–1975.

tance, although even this fishery was already in decline by 1973. A major benefit of striped bass to commercial fishermen was its availability prior to the shad run in the spring, and in the fall as well; the fishing season could thus be extended. In 1976, reports of elevated levels of polychlorinated biphenyls (PCB) in the flesh of many fish species prompted closure for fisheries above the Troy Dam, and for commercial landings below the dam except for shad, sturgeon >48 inches (122 cm), and goldfish sold for ornamental use (Brandt 1981). In 1982, the fishery re-opened for Atlantic tomcod, alewife, blueback herring, and rainbow smelt. Evidence for renewed interest in the Hudson River fishery comes from a NYSDEC report (Horn and Skinner 1985) that listed the total 1983 fish harvest from the Hudson as 252 t, up from the average of 105 t for 1965–78 (Sheppard 1983). In 1983, 666 licensed commercial fishermen participated in the Hudson River fishery, of which 542 were scap-netters, fishing for bait or personal use (Horn and Skinner 1985). This is also an increase over the 1970–79 average of 488 fishermen (including 441 fishing with scap nets) (Sheppard 1983).

Despite the diminished role of the Hudson River fishery in the statewide striped bass commercial activity, the re-opening of this fishery is considered a top priority and will be done as soon as health risks from PCB levels fall below the U.S. Food and Drug Administration (FDA) tolerance of 2.0 ppm (2.0 $\text{mg}\cdot\text{L}^{-1}$). However, in May 1986, the DEC extended the ban on striped bass fishing to include fish from all parts of New York State, including western Long Island (NYSDEC News Release, May 6, 1986). The action was taken because of PCB levels in 444 striped bass from marine waters of New York State indicated that legal-sized fish (24 in. (61 cm)) throughout the marine fishery had PCB levels in excess of the FDA tolerance (Sloan et al. 1986). A follow-up survey of more than 800 striped bass was conducted in 1987 (E. Horn, NYS Department of Health, Albany NY, pers. comm.).

Recreational — Recreational fishing can be divided into three regions: upper river (south to the Troy Dam), upper estuary (Troy Dam to Poughkeepsie), and the lower estuary (Sheppard 1976). In the upper region, sport and recreational fishing exist alongside heavy industrial activity in certain stretches of the river, in particular near Corinth (351 km), Hudson Falls (319 km), and Fort Edward (314 km). A 1932 biological survey noted the presence of severe pollution from pulp and paper mills, other industries, and municipalities, and recognized the harm of such wastes to fish life (NYS Conservation Dept. 1933). Nevertheless, brown and brook trout, rock bass, large- and smallmouth bass, common carp, white sucker, American eel, brown bullhead, yellow perch, walleye, northern pike, chain pickerel, bluegill, pumpkinseed, and redbreast sunfish were noted as popular food and game species.

Information following the 1932 survey is scant. An inventory in 1969 between Fort Edward and Lock 1 (km 156) by Lane (1970), cited in Sheppard (1976) found no significant fishery, and only juveniles of gamefish were collected in the river channel. Juvenile rock bass, pumpkinseed, yellow perch, walleye, and chain pickerel also dominated collections taken in the mid-1970's for PCB analysis, leading Sheppard (1976) to speculate that "some unknown factor is causing the exodus or the demise of the mature segment of certain fish populations...". Despite the unexplained decline, anecdotal evidence from regional fishery personnel suggested that the upriver fishery improved in the years up to 1976. Following the discovery of PCB in the entire ecosystem below Hudson Falls, the freshwater fishery from that point downwards has been closed indefinitely.

The mid-Hudson recreational fishery consists of all the game/food fish species of the upper region, together with black crappie, striped bass, rainbow smelt, blueback herring, and alewife (NYS Conservation Dept. 1937; Sheppard 1976). In the lower reaches, large and smallmouth bass, stripes bass, white perch, American shad, river herring Gaspereau, and white catfish dominate the sport fishery, with lesser interest in Atlantic tomcod, bluefish, summer and winter flounder, and weakfish. Largemouth and smallmouth bass currently are the most valuable recreational species in the river. Since 1977, the estuary has been the focus of a state Bass Angler Sportsmen's Society (B.A.S.S.) fishing tournament. Also, since 1981, an active campaign by DEC to stimulate a recreational shad fishery has been fairly successful (Brandt 1985).

Sheppard (1976) calculated values for the present and potential commercial and recreational fisheries. For these analyses, estimates were included of the contribution of

TABLE 5. Potential annual values of Hudson River fisheries, and potential contribution to saltwater fisheries. (Estimates assembled by Sheppard 1976).

A. Commercial

Species	Potential Catch (t)	Value (1000 $)
American shad	455 - 682	200 - 300
Striped bass	23 - 45	20 - 40
White perch	23 - 45	12.5 - 35
American eel	23 - 45	10 - 20
Herring, Alewife	23 - 45	4.5 - 6
Rainbow smelt	9.1 - 14	8 - 12
Sturgeon	6.8 - 9.1	4.5 - 6
Atlantic tomcod	2.3 - 6.8	1.5 - 15
Total	*565 - 892*	*261 - 434*

B. Recreational

River Reach	Estimated Production (#/ha)	No. of Angler Days[a]	Value of Angler Days[a] $10.00	$12.50	$15.00
Upper	40.5	53	0.53	0.66	0.80
	81.0	107	1.07	1.34	1.60
	121.4	160	1.60	2.00	2.40
Middle	60.7	440	4.40	5.50	6.60
	121.4	880	8.80	11.00	13.20
	161.9	1173	11.73	14.60	17.60
Lower	Total estimated recreational/sport value = $1.65 million				

C. Contribution to Marine Fisheries

Commercial: $173,000 to $1 million

Recreational: $28 million to $48 million

[a] Assumes a recreational usage of 20 % of the estimated annual production, and a per capita catch rate of 0.7 kg/angler.

Hudson stocks to saltwater fisheries beyond the estuary. Data were poor, so a number of indirect estimation methods and reasonable guesses had to be used (Table 5). Recreational fishery potential took the form of a sensitivity analysis, and used different assumed levels of fish production, percent utilization of the standing crop of fish for recreation, average dollar value of an angler-day, and daily per capita catch rate.

Management of the Hudson

Management policies have evolved over the course of the last 150 years. Resource development and exploitation served as the early emphasis, and included development of water resources for transportation, drinking water, industry, and power generation as well as fisheries. As the pressures from a growing population increased and one use began to conflict with another, management was forced to consider multiple objectives. Conservation of the natural resources of the Hudson River Basin gradually became a part of management planning.

The "management" of the Hudson evolved from a series of large-scale events, interspersed with smaller, more easily anticipated events. The large-scale issues often represented activities without precedent in the Basin, and therefore forced the creation of policy and regulation. To a certain extent, issues in the Hudson also contributed to the development of policy at the national level, which in turn helped to set guidelines for state legislation.

Over the past 20 years, three major issues arose that sparked major controversies over environmental management policies. First, the rapid and extensive construction of power stations in the mid-section of the estuary, slated for completion in the early 1970's, posed early-recognized conflicts with the fishery there (*Scenic Hudson Preservation Conference* v. *Federal Power Commission*, 354 F.2d 608 [2nd Cir. 1965]). Second, the 1974 "discovery" of great quantities of PCB in the Hudson prompted a massive assessment project and years of developing a remedial action plan. Finally, a proposal to dredge and fill a substantial portion (93 ha) of the mouth of the estuary around Manhattan Island, to rebuild a highway and obtain Federal aid for the City of New York, became a major test of environmental protection laws. These issues represent the kinds of development impacts that impinge on most settled estuaries, and for this reason they formed the focus of case studies of the efficacy of environmental impact assessment (Limburg et al. 1986a; Barnthouse et al. 1988b). A description of management of the Hudson, even emphasizing development of fishery resources, is incomplete without consideration of these important events.

A fourth issue of equal weight is the release and fate of toxic substances in the environment of the Hudson; however the records of releases are poorer than fishery statistics, and much of the most important work is being done through historical reconstruction (e.g., Ayres and Rod 1986).

Legislative Background: the Mandates for Environmental Assessment

Several pieces of legislation have featured in the recent managerial history of the Hudson (Limburg 1985). However, it was the *National Environmental Policy Act* of 1969 (NEPA), that first clearly enunciated the necessity of scientific investigations to determine environmental impacts. The goals of NEPA were to insure careful assessment of major, federally funded or regulated projects; thus, NEPA established a framework within which applied environmental science should operate.

Two other Federal environmental protection laws have played major roles in guiding research on the Hudson. The *1899 Rivers and Harbors Act* originally legislated to maintain navigable waterways, was resurrected by Hudson River environmentalists in the 1960's to circumvent industrial pollutant discharges into the river. The *Federal Water Pollution Control Act* (as amended in 1972), also referred to as the Clean Water Act or CWA, replaced sections of "Old 1899" pertaining to discharge of pullutants and dredge permits, as well as authorized construction of sewage treatment plants and other technological controls on pollutants.

A fourth law to influence research in the *Coastal Zone Management Act* of 1972 (CZMA), which has been implemented in New York State since 1982. CZMA directs coastal states to develop and implement management programs "to achieve wise use of the land and water resources of the coastal zone giving full consideration to ecological, cultural, historic, and esthetic values as well as to needs for economic development" (CZMA, 16 U.S.C. Sections 1451 et seq., Sect. 303). The Act further mandates the establishment of estuarine sanctuaries in which to conduct research to increase understanding of the ecology of the coastal zone. Because of its recent implementation in the Hudson River, CZMA has not had the historical impact of the preceding laws. However, it will likely affect the tone of future scientific research in the Hudson. The Hudson River National Estuarine Research Reserve (HRNERR) was established in 1982 and consists of four sanctuaries in the estuarine portion of the river. In 1986–87, in accordance with CZMA, the State renovated a research station in the vicinity of Tivoli Marsh (km 160); the station, along with a combination of private and Federal monies, are available for education and research in the HRNERR.

At the State level, the major body of legislation to have had direct bearing upon environmental issues in the Hudson is the Environmental Conservation Law of the State of New York (ECL). Various articles and titles under the ECL set forth the mandates for envrionmental protection. Sections of greatest relevance to the Hudson include water pollution control legislation, Article 17; State Environmental Quality Review (SEQR), Article 8; protection of water resources, Article 15; Freshwater Wetlands Act, Article 24; and the Hudson River Fisheries Management Program, Section 11-0306, repealed in 1987 and replaced by Hudson River Estuary Management Program. Some of these statutes are implementations of Federal laws, as was the intent of Congress.

Case Studies: Power Plants, PCB, Westway, and Toxic Substances

Environmental Assessment of Power Plants

The questions of impacts of five power generation stations plus one proposed station in the mesohaline portion of the Hudson (Fig. 10) were studied and debated for 17 yr. At a cost in the tens of millions of dollars, the scientific

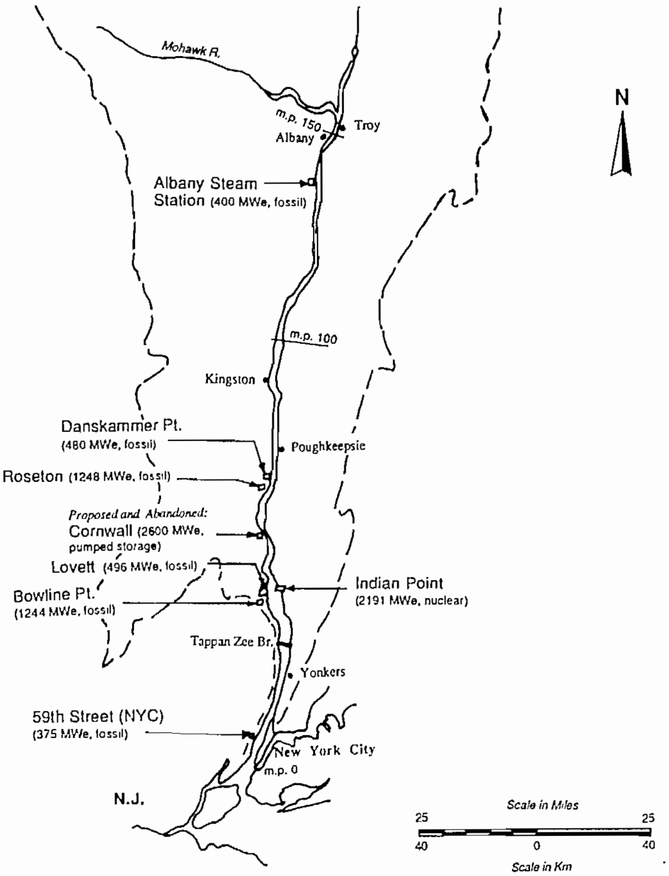


FIG. 10. Locations of power generating stations along the Hudson.

research failed to reach any unambiguous conclusions regarding the extent of potential, long-term impacts. Yet, in 1980, after years of litigation and no clear decision in sight over the critical need for cooling towers, an out-of-court settlement was reached among the major conflicting parties (Sandler and Schoenbrod 1981; Talbot 1983). The Hudson River Agreement laid out five following major provisions that included concessions both to utilities and their opponents. Additionally, funds were set aside for research and monitoring (Sandler and Schoenbrod 1981). The Agreement, now considered a unique historic decision, was reached only after all routes of assessment failed.

It was determined at a fairly stage in the assessment procedures that the major impacts would be the impingement of organisms on the cooling water intake screens and entrainment through the power plants (particularly larval and juvenile fish) (Barnthouse et al. 1984). Eventually, as the issues narrowed the focus onto fish, particularly striped bass, the percent reduction in fish population size due to operation of the power plants became the critical question. High variability in the estimates of year-class success of these fish species, together with a poor understanding of their population biology, made obtaining the answer to this question most difficult. Theories of fish population biology, by no means uncontested among fisheries scientists, were brought forth to add another layer of controversy. For example, if density compensation (the ability of fish populations reduced to low densities to recover) was operative, how did it work, and how much would it offset increased mortality from the power plants? Whereas the utilities' consultants contended that this phenomenon was very important (e.g., Lawler 1974), numerous witnesses for the regulatory agencies felt that the evidence for it was conjectural and that any effect was unquantifiable, given the absence of substantive data (e.g., Levin 1979; Slobodkin 1979).

Another important question involved the ability to observe adverse effects on the fish stocks in the face of other significant factors. How responsive were the fish to environmental factors, and to what degree were their populations regulated by temperature, water flow, food availability, etc.? Would it even be possible to detect a negative effect from operation of the power plants, if environmental variability were high? Certainly there was evidence of the importance of environmental factors, especially hydrologic regimes, in two other studies, one in the Chesapeake Bay (Mihursky et al. 1981) and the other in the San Joaquin estuary (Chakwick et al. 1977). However, although both studies used multiple linear regression techniques, and came up with similar results, the mechanisms of influence on fish stocks were entirely different and therefore direct comparison of these studies would be misleading (Limburg et al. 1986a). From multiple regression studies performed at Texas Instruments, Klauda et al. (1980) suggested that while certain combinations of factors appeared to be important, it was not clear that any single factor or combination was consistently critical. Thus the issue of environmental influences remains unresolved, and the original question (importance of human vs. natural forces) may be intractable.

Much of the field assessment was carried out to provide input to numerical models of the Hudson River fish stocks. Models were used heavily as tools by both utilities and their litigative opponents (the Neclear Regulatory Agency and the Environmental Protection Agency) to demonstrate the effects of power plants on the long-term dynamics of major fish populations.

Beginning in the late 1960's and spanning the 1970's, a series of mathematical models was developed in the hopes of combining the numerous plausible factors influencing major fish populations, in particular striped bass. The modelling efforts began with fairly simplistic (and erroneous) formulations (Hudson River Policy Committee 1968) and evolved to increasingly complex formulations. Life-history details of fish were incorporated (Lawler 1972a). Hydrodynamic terms, first in one dimension (Lawler 1972b), and later on in two (McFadden and Lawler 1977), were included to simulate the movement of fish eggs and larvae up and down the estuary past the power plants. At the same time, massive field sampling surveys collected data to calibrate and test the models (Christensen et al. 1981).

The additional complexity added to the models did not improve the fit of their computed results and the data sets with which they were calibrated. This led to the development of additional terms to correct for the discrepancies between observations and predictions (Christensen et al. 1981). The way the terms were developed by the utilities' consultants and those advising the regulatory agencies employed different assumptions that contributed to the divergent answers produced by the opposing models. One of the biggest differences between utility and agency models lay in the former's assumption of density compensation in fish population dynamics (Swartzman et al. 1978). This tended to offset the losses of eggs and young fish with enhanced survival of the remaining stock. Model predictions often diverged by an order of magnitude (Limburg et al. 1986a).

It is important to realize that the modelling efforts were driven largely by court orders in the licensing hearings. As pointed out by Barnthouse et al. (1984), the development of research studies was governed by the institutional framework of NEPA, and judgment of results of studies was not through scientific peer review but rather through the legal process. Courtroom examination, they write, is very good at finding weaknesses in reasoning and at catching the obviously dishonest statement; but the judicial process also discouraged communication among scientists, and led them to develop one-sided arguments (Barnthouse et al. 1988a). Thus, the constraints of the legal system trapped all parties into advocacy roles, even when the accumulated evidence suggested that such positions were unreasonable. The ability of the collective adversarial groups to break the "vicious circle" they found themselves in, by negotiating the Hudson River Settlement, represented a novel solution that saved them millions of dollars in further legal confrontation.

PCB

In the case of PCB contamination of the Hudson, a startling fact was discovered in the early 1970's: a manufacturing company in the upper Hudson (General Electric Co.) had been discharging PCB, compounds that were only just beginning to be recognized as a global environmental hazard, into the river for the previous 30 years. Even as the seriousness of the situation became apparent, two catastrophic events occurred to compound the problem. The first was a dam removal at Fort Edward in 1973, behind which deep layers of PCB-contaminated sediments had built up; removal had the combined effect of lowering the water level, exposing many bankside deposits of PCB-contaminated sediments, and of washing materials downstream. The second event was a 100-yr flood in 1976 that washed even more material downstream (Horn et al. 1979). By 1983, an estimated 270 t of PCB remained in the entire river of perhaps 610 t discharged in total (HRF 1984). All during the 1970's, from the period of initial discovery, through the courtroom proceedings to determine the level of violation and its ultimate settlement, and into the 1980's, much of the research that has been carried out has served to establish where the PCB were located and how they moved about.

Following a PCB Settlement Agreement (NYSDEC, 1976), a special advisory committee was established to determine the extent of contamination and recommend mitigation. The fundamental question was, *should* the PCB be removed from the Hudson? Unfortunately, providing answers has required more time than originally thought. Although dredging in areas of high PCB concentration was recommended by the advisory committee (Sanders 1982), siting a dredge spoil depository brought objections from local interests; a final mitigation plan is yet to be implemented.

Part of the difficulty has lain in understanding the physical and biological mechanisms of transporting PCB. With physical transport, there has been a question of whether the contaminated sediments are borne as a uniform or as a graded suspension (J.E. Sanders, Geology Dept., Barnard College, pers. comm.; HRD 1984). In the former case (Fig. 11), if the sediments are transported more-or-less directly from the pool of heaviest concentration (above the Thompson Island dam) to the estuary, then dredging in that pool and capping remnant shoreline deposits would go a long way to solving the problem in the river. If, instead, the graded suspension hypothesis proves true, then dredging efforts would have to be extended over a larger portion of the upper Hudson and would be far less efficient.

Other uncertainties concerned the biological fate of PCB, meaning their transport through the food web, direct sportive uptake, and even their transformation into compounds of varying toxicity. Relatively early on it was thought that the main mechanism of biological PCB transport was via the food chain (Nadeau and Davis 1974); the implications of biological uptake were investigated in a numerical simulation study that coupled a physical transport model of PCB into and throughout the estuary with a biological food web model (Hydroscience 1979). That model projected higher concentrations of PCB in upper trophic levels (fish, especially striped bass) than has actually proven to be the case (Limburg 1984).

The primary effect of PCB contamination was the closure of the striped bass commercial fishery and prohibition of recreational fishing in a 160 km stretch of river. Commercial fishermen and anglers have criticized the management actions rather than the contamination. It has been difficult to show that any single transport process dominates, or that any species has been exposed directly to grave danger, with the possible exception of cancer risks to Atlantic tomcod (Smith et al. 1979; Klauda et al. 1981; Dey et al. 1986). It has been equally difficult to motivate a PCB removal program, given the objections of upriver residents who do not wish to live near a PCB disposal site.

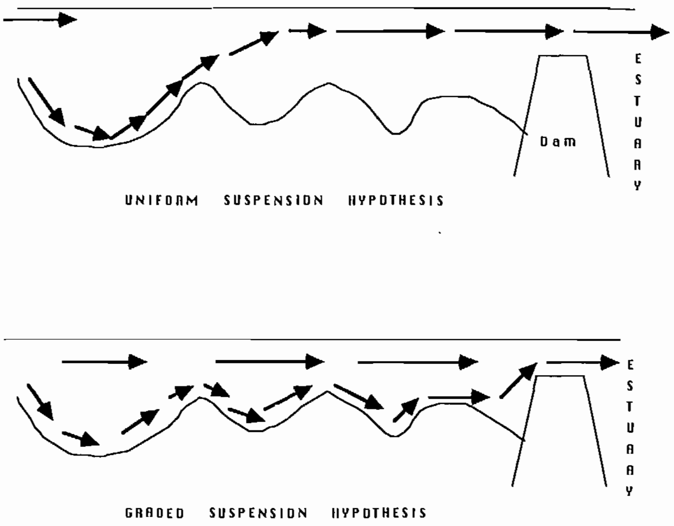


FIG. 11. Two hypotheses used to describe possible sediment transport from pool of high PCB concentration down to the Hudson River estuary. The uniform suspension hypothesis (*top*) holds that PCBs adhering to sediments from that pool travel evenly to the dam that separates the upper Hudson from the estuary. The graded suspension hypothesis (*bottom*) states that PCBs travel from one pool to the next via scouring processes.

Westway

Controversy characterized the 12 years of scientific research along the proposed Westway project area and much of the lower Hudson. Westway originated in 1956 in recognition of the need to rebuild New York City's decaying West Side Highway. Running from southern tip of Manhattan north to 72nd Street, part of the highway was closed in 1973 following a collapse of an elevated portion. By 1974, a Westway Project proposal was in place that combined highway rebuilding with substantial urban renewal (Limburg et al. 1986a). A 4.2 mi. (6.7 km) stretch of highway would be constructed partly in fill that would extend more than 200 acres (ca. 85 ha) into the river itself. Atop the fill, parkland and prime real estate would be created. The fill and an additional 10 acre (4 ha) platform would occupy roughly 10% of the cross-sectional area of the river, obliterating a section of decaying, abandoned piers. Funding for 90% of the project would come from the Federal Highway Administration (FHWA) under legislation for the construction of interstate highways (FHWA 1977).

Under Section 404 of the "Clean Water Act", and §10 of the River and Harbors Appropriations Act, the New York State Department of Transportation (DOT) was required to obtain a dredging permit; this was applied for to the U.S. Army Corps of Engineers in 1977. An environmental impact statement evaluation (EIS) was prepared jointly by the FHWA and the DOT (FHWA 1977).

Perhaps the most significant ecological finding, reflected in the initial EIS evaluation and all subsequent studies, is that the lower estuary around New York City supports a far more viable and diverse ecosystem than most parties had imagined. More suitable habitat exists in the region for commercially important fish, such as winter flounder and striped bass, than previously thought. The initial biological survey came to the unexpected conclusion that a "full cycle of biological food chain exists", beginning with primary producers and containing a rich benthic community, and culminating in "fish and subsequently the birds or larger fish which prey on these small fish" (Alpine Geophysical Associates 1974).

Further studies showed a diverse fish community in the region of the proposed project. Atlantic tomcod, hogchoker, bay anchovy, winter flounder, striped bass, and white perch were all found in the area in a 1980 survey, and the latter three species showed a preference for the so-called "interpier area" (the site of the abandoned piers, scheduled to be removed as part of the Westway project) (LMS 1980). Although not directly stated in any reports, it could be seen from the data that the area slated for Westway contained the largest concentrations of striped bass of any of the sample sites (Limburg et al. 1986a). This fact became a key issue in litigation.

Several groups initiated lawsuits against the West Side Highway Project, questioning the adequacy and legality of the environmental assessment process (*ART v. West Side Highway Project, 536 F. Supp. 1225* [S.D.N.Y 1982]; *Sierra Club v. U.S. Army Corps of Engineers, 701 F. 2d 1011* [*2d Cir. 1983*]). At issue were questions of air pollution, noise pollution, and fisheries impacts. Eventually the only consideration given weight by the court was whether or not impacts on the striped bass population were adequately addressed. As in the case of assessing power plant impacts, scientists engaged by resource management agencies differed greatly from those working for the project applicants in their opinions regarding impacts. Objectivity of the scientific assessment studies was called into question during cross-examination (e.g., Fletcher 1981), when it was shown that data were intentionally presented as court evidence in such a way as to diminish the importance of the Westway interpier area.

What, however, is the Westway area's role? As habitat for fish, is it important as a sheltering spot, as a food source, or some congenial combination of factors? Is the area of critical importance to striped bass, as suggested by the Sierra Club and other parties (*Sierra Club v. U.S. Army Corps of Engineers, 701 F. 2d 1011* [*2d Cir. 1983*]), or is it not, as suggested by the hypotheses proposed by proponents of and consultants to the Westway project (*ART v. West Side Highway Project, 536 F. Supp. 1225* [*S.D.N.Y 1982*])? The data simply do not exist to confirm or reject any hypotheses at this point. In the end, after massive pressure in Congress, the Governor of New York and the Mayor of New York City agreed to abandon the Westway in favor of a reduced and environmentally less disruptive plan.

Toxicants

Over the last 100 years, a wide variety of materials now known to be toxic to humans and other organisms have been discharged in the Hudson Basin and adjacent metropolitan watersheds (Raritan River, Arthur Kill, and Passaic River). However, it was not until the passage of the Toxic Substances Control Act in 1976 that a national mandate for toxic pollution control existed. The EPA published a list of "priority pollutants" in 1973, but promulgation of enforceable standards lagged by a number of years. New York State did not set standards until 1984 (Rohmann et al. 1985).

In the Hudson and adjacent Raritan Basins, record-keeping has been poor. Even after the 1974 establishment of the State Pollutant Discharge Elimination System (SPDES) program to register point-source polluters, reporting largely has been a failure. A study of toxic pollution in the Hudson Basin by Rohmann et al. (1985) found records of 555 separate discharges of 26 major toxic chemicals, including 25 EPA priority pollutants and oil and grease. Of the discharges, 40% were unpermitted, even though 78 of them contained known or suspected carcinogens. Rohmann et al. (1985) also found only 102 discharges to have sufficient information for quantifying their magnitudes. Review of regulatory data bases revealed many errors, inconsistencies, data omissions, and a general lack of consistent reporting standards.

Non-point-source releases of toxicants have been even more difficult to quantify. However, attempts have been made (Ayres et al. 1985; Ayres and Rod 1986) to reconstruct historical loading trends of heavy metals, pesticides and herbicides, and PCB, PAHs, oil, and sewage wastes in the Hudson-Raritan Basin. Theirs was a mass balance approach, tracing pollutants from four general source types (metallurgical operations, fossil-fuel combustion, consumer end uses, and industry) through deposition on four land-use categories (developed land with combined sewage and storm drainage, developed land with separate conduits, agricultural cropland, and undeveloped land). Where site-specific data were unavailable, national statistics were pro-

TABLE 6. Estimates of pesticide (A) and heavy metals (B) loadings into the Hudson-Raritan Basin (from Ayres and Rod 1986). (Metric tons per year).

A. Pesticides

Year	DDT	Lindane	Aldrin	Chlordane	Dieldrin	Endrin	Heptachlor	Toxaphene
1980	1.9	0.08	0.001	2.8	0.005	0.001	0.025	0.020
1976	2.4	0.21	0.006	5.6	0.021	0.005	0.023	0.041
1971	3.5	0.28	0.010	8.5	0.030	0.007	0.026	0.050
1966	4.6	0.50	0.014	6.2	0.064	0.010	0.025	0.052
1964	4.7	0.64	0.010	5.5	0.066	0.010	0.023	0.054
1960	5.0	1.20	0.006	5.1	0.078	0.012	0.022	0.053
1955	3.4	2.00	0.003	4.4	0.067	0.011	0.019	0.053
1950	2.5	1.70	0.001	3.1	0.003	0.004	0.014	0.037
1945	1.1	0.10	—	0.2	—	—	—	—

B. Heavy Metals

Year	As	Cd	Cr	Cu	Pb	Hg	Ag	Zn
1980	280	60	430	1500	2500	5	4.0	3600
1970	440	140	750	1700	3500	9	3.3	4700
1960	380	110	770	1300	3000	5	2.5	3800
1950	420	93	660	1500	2800	5	2.3	3800
1940	600	83	680	1700	2700	5	1.1	3500
1930	850	47	210	740	1600	4	0.7	2700
1920	230	48	220	820	1600	3	0.5	1800
1900	64	18	210	610	250	2	0.2	490
1880	15	6	52	210	10	2	0.1	160

rated by land-use type and population densities. Models then were used to estimate loading rates to the rivers. Table 6, adapted from Ayres and Rod (1986), presents estimates of pesticide and metal loadings into the basin. Although considerable uncertainty is associated with them, loadings for most materials are estimated to have declined since the imposition of regulatory programs.

Given the difficulties in obtaining accurate information on toxic substances, how are risks perceived by users of the rivers? Among those at greatest risk are consumers of fish. In 1983, the New Jersey Department of Environmental Protection conducted a multidisciplinary study of fish contamination and risk perception (Belton et al. 1985). This study measured levels of PCB and pesticides in popular game and food fish from the lower Hudson, New York Bay, and upper Newark Bay areas. Their findings were compared to models of human health risks developed by the EPA and FDA to estimate risks of cancer to consumers. At the same time, fishermen and crabbers were surveyed to find out their attitudes and perception of risk.

PCB levels exceeded the FDA tolerance (2 $\mu g \cdot g^{-1}$) in 6 species: white perch (mean = 4.87 $\mu g \cdot g^{-1}$), white catfish (mean = 4.87 $\mu g \cdot g^{-1}$), striped bass (mean = 3.49 $\mu g \cdot g^{-1}$), American eel (mean = 3.45 $\mu g \cdot g^{-1}$), bluefish (mean = 3.45 $\mu g \cdot g^{-1}$), and blue crab (mean = 2.08 $\mu g \cdot g^{-1}$) (Belton et al. 1985). A risk calculation based on the EPA model predicted high probabilities of cancers resulting from lifetime consumption of these fish, yet fishermen had a relatively low perception of this risk. Of the fishermen surveyed (total not given), 61 % were retirees, and 44 % were predominantly lower-income workers 20–49 years of age. 59 % of those surveyed fished primarily for consumption. More fishermen (46 %) thought the fish were safe to eat than those who did not (35 %), even though most were aware of official consumption advisories. Over half of those who did not eat their catch did so out of health concerns, while one-third of those who did eat the fish felt they were probably eating contaminated food, but did so regardless.

Fishery Management Program

The years of fisheries-related research carried out for the assessment of power plant impacts, together with growing fears over PCB and other toxic contamination, made clear that a more comprehensive fisheries management plan was needed for the Hudson. In July 1979, legislation was signed to create the Hudson River Fishery Management Program, to have jurisdiction over the estuarine portion of the Hudson, "with consideration of the remainder of the Hudson River, New York Bight, and Long Island Sound insofar as they impact the Hudson River fishery..." (§ 11-0306, NYS ECL). No special program was established for the upper Hudson *per se*.

An initial evaluation of needs, as mandated by § 11-0306, was carried out by W. Dovel for the DEC (Oceanic Society 1980). This study cited the lack of an understanding of the total ecosystem of the Hudson as the greatest barrier to effective fishery management. An ambitious set of recommendations included a list of long-range goals, centering on development of an "optimal yield" fishery for both commercial and recreational users, restoration of a shell fishery, establishment of a funding system for research and management, and the general promotion of fish as a natural resource. Water quality monitoring, gear restrictions, aquaculture development, interpretive educational programs, and establishment both of a special DEC field station and of an advisory group were among the recommendations.

The report also highlighted critical areas for research and regulation.

The DEC made public a Hudson Estuary Fisheries Development Program in 1980, with the stated goals of restoring and maintaining the "ecological health" of the river and managing it for optimum sustained yield (Brandt 1981). Among the objectives set were: improvement of information archiving, data processing, and data retrieval; improvement of catch, effort, and life-history information for American shad; improvement of reporting on commercial catches in general; continued monitoring of selected fish and invertebrates for PCB contamination; encouragement of recreational fishing for American shad, alewife, blueback herring, and rainbow smelt; and advising as necessary on various directed management programs (Brandt 1981).

A Hudson River Fisheries Advisory Committee was also established in accordance with the law. The committee, composed of DEC fisheries biologists and managers, fishermen, scientists, and interested laypersons, met on a monthly basis since 1979 to discuss issues of importance to fisheries management. In 1984, the Commissioner of Environmental Conservation created a special position for a Hudson River Coordinator to oversee the State's Estuarine Sanctuary Program and act as a liason between the State and other interest groups.

In the years following adoption of a management program, the State has maintained a number of investigatory and monitoring activities. A project was carried out until 1985 to determine characteristics of the Hudson River striped bass population, in conjunction with a larger-scale study of the health of American East Coast striped bass stocks coordinated by the U.S. National Marine Fisheries Service. Other monitoring programs have been carried out for an additional eight species (Table 7). Abundances of American shad have been monitored in order to develop an index of year-class strength. Several fish species, including striped bass, pumpkinseed, and black bass, have been monitored for PCB and other toxic compounds. Impingement and entrainment studies are being carried out at power plants in accordance with the 1980 Hudson River Agreement.

In 1987, the State repealed the Fishery Management Program and replaced it with a Hudson River Estuary Management Program, in which "it is hereby declared to be the policy of the State to preserve, protect and, where possible, restore and enhance the natural resources, the species, the habitat and the commercial and recreational values of the Hudson River estuary" (ECL § 11-0306). The new program promises to approach fisheries management from a broader perspective than management of individual fish populations.

The Future of Management on the Hudson River

The Dovel report (Oceanic Society 1980) decried the lack of an understanding of the Hudson as an ecosystem, stating that this represented a serious hindrance of fisheries management. The argument was not new; Howells et al. (1970) voiced the same concern nearly a decade before. An ecosystem approach — one that relates biotic and abiotic parts of ecosystems together through understanding of processes and structuring — also was advocated by Limburg et al. (1986b) for environmental impact assessment. Such an approach is inherently hierarchical, focusing on one scale of resolution or another as necessary to the problem at hand. Others (see Barnthouse et al. 1988a), while recognizing the importance of understanding the ecosystem, argue that the practicalities of funding and directing research do not make this approach feasible. They claim that so much time and money was spent on attempts to evaluate details of the life-history characteristics of even a few species of fish that the prospects of greater understanding are dim.

However, to recognize the importance of the ecosystem approach while arguing that only the more narrow approach is practicable is an unnecessarily pessimistic point of view, and one not likely to lead to useful answers if applied generally. For fisheries management as well as environmental impact assessment, a view that recognizes the multiplicity of spatial, temporal, and organizational scales is critical; the organisms of interest cannot be studied in isolation of its habitat. Similarly, research efforts must reconcile information from a spectrum of studies ranging from highly controlled, ecologically unrealistic studies such as laboratory bioassays to very realistic investigations, such as field studies, that defy replication. By combining such studies with controlled microcosms and mesocosms and the improvement of modelling capabilities, we must seek to improve our capacity to extrapolate and to predict. At the same time, it must be acknowledged that there are limits to predictability and that management must be carried out with

TABLE 7. Data collected by the Hudson River Fisheries Unit, NYSDEC, on the Hudson River estuary, 1980–85.

	Juvenile abundance		Commercial Catch			Haul Seine	
Fish species	Bottom Trawl	Beach seine	Biochar[a]	Age	Catch/effort[b]	Biochar[a]	Age
Blueback herring		X					
Alewife		X					
American shad		X	X	X	X	X	X
White perch	X	X					
Striped bass	X	X	X	X	X	X	X
Largemouth bass						X	X
Smallmouth bass						X	X
Bluefish	X						
Weakfish	X						

[a] Biocharacteristics include fork length, total length, and weight.

[b] Catch per unit effort is defined as number per 1000 yd^2 in gill net.

some degree of uncertainty. Monitoring coupled with a flexible management scheme that allows for the mitigation of undesired consequences are essential components of a sound management scheme (Limburg et al. 1986b).

Despite the intense pollution and fishing activity that has befallen the Hudson at times, the system appears to be a resilient one, to judge from such indirect indicators as species abundances and stock size indexes. This may be related to the flushing characteristics of the estuary: unlike estuaries with large, velocity-reducing deltas, the Hudson is more like a pipe that flushes materials from its watershed out in the spring and is invaded by the sea in the summer. The geology of the watershed may contribute to ecosystem resilience through chemical buffering by anions; one factor that might help explain the differences between stock abundances of anadromous fish in the Hudson vs. other East Coast rivers is the difference in watershed buffering capacities. A third factor may be the nutrient enrichment from New York City, whose sewage is washed out and dispersed into the New York Bight. Finally, the 10-yr partial ban on fishing has reduced fishing pressure effects on several populations of fish.

At this point, it is impossible to make any statements as to which of these factors, if any, is the "master variable" controlling the ecological dynamics of the Hudson. There is still an incomplete understanding of how the Hudson behaves as an ecosystem, whether it is chronically stressed or not, whether it is one with tight couplings among components, etc.

As scientists, we can argue that much more basic research is needed. But, as managers, we must also acknowledge that problems have to be dealt with on different timetables, some immediately, some in the long term. Therefore, a successful management policy on the Hudson would have to marry these two objectives — understanding and execution of programs — in a way that they would complement and enrich one another.

As ecosystems scientists, we may identify some of the research needs that, if satisfied, might substantially improve understanding of ecosystem aspects of the river. These areas of research would substantially improve the knowledge base from which fishery decisions must be produced, as they impinge directly or indirectly on the well-being of fish populations using the ecosystem.

The magnitude and types of primary and secondary production, together with net imports, set the energetic boundaries within which other organisms (including humans) must operate — one cannot extract more energy, e.g. in fish harvests, from a system than what goes in. Thus a basic understanding of production and its controls is a fundamental and important step. In the Hudson, fairly extensive productivity investigations were carried out below the Tappan Zee Bridge (Sirois and Fredrick 1978; Thomas et al. 1976; Malone 1977). Studies of the upper estuary and freshwater reaches of the Hudson are underway (HRF 1987, 1988). Neither links between trophic levels, nor processes (e.g., species succession and competition) operating within levels, are well understood and integrated.

Better estimates are needed of standing stocks, turnover times, and spatiotemporal dynamics of important species or communities of organisms. Much of the biological data collected for the power plant impact assessments did not quantify biomass and production rates, or provide budgets, from which calculations and comparisons could be made. The spatiotemporal extent of ecological communities important as fish habitat, coupled together with an understanding of actual and/or potential uses of the habitat, are important data for a fisheries management program. Many of the results of the numerous biological and ecological studies that were carried out for environmental impact assessment suffered the fate of burial in unpublished reports; efforts have been made to resurrect and publish some of this information (Barnthouse et al. 1988b; Limburg et al. 1986a; Smith 1987), but more remains.

Relationships of the estuarine/riverine system to the surrounding watershed and, at local scales, relationships of individual tributaries and associated watersheds to the river and estuary must be better understood. Very little up-to-date information exists on levels of materials entering the Hudson from the watershed; for example materials budgets for nutrients are based largely on estimates made years ago. A project to provide newer estimates and recompute carbon and nutrient budgets has been undertaken, however (Fruci and Howarth 1988). Budgets for toxic materials disposed of in the watershed are sorely in need of updating; most of the records of toxic waste disposal are sketchy, if even in existence. As the downstream recipient of materials from the watershed, the Hudson's ecology is affected directly and indirectly by natural and societal activities there. Fate and transport of toxics, and the potential impacts or bufferings from acid precipitation, remain as important questions.

Similarly, the relationship of the upper Hudson, and its tributaries, to the lower Hudson should specifically be addressed. So much of the upper Hudson is controlled in the canal and locks system of the Champlain Barge Canal that there is a tendency to overlook its ecological importance. Yet, as seen in the case of PCB release, activity in the upper river can have severe adverse effects in the estuary. In another light, if fisheries management is to consider reestablishing means for anadromous fish to enter the upper Hudson, e.g., through the use of lifts, a knowledge of the productive capacity of the riverine ecosystem would greatly aid planning for fishing programs.

In an applied ecological framework, the question of cumulative impacts of human activities has yet to be adequately addressed. For instance, if the proposed Westway project had in fact been granted permission to proceed, what would the additional impact of this stress have been on the striped bass population? Do thresholds exist, beyond which some ecological entity or process ceases to exist or changes radically? A second aspect of development is its tendency to generate even more growth. With competition for resources occurring in the market place, the action of one party in altering a part of the ecosystem may hurt another party, or conversely may even stimulate more development. This was evident in the comments of the State of New Jersey on the environmental impact statement review for Westway (COE and FHWA 1984) that perceived the "using up" of striped bass habitat by New York City as an opportunity loss for development on the New Jersey shore.

Improvement in record-keeping for toxic pollutants and their eventual discharge into the Hudson, as well as physical habitat alteration in the watershed, should be accorded high priority. The investigations carried out to date by independent groups have shown that, although the information is sketchy, there is reason for concern about the fate of toxic substances in the Hudson environment. The results of water quality monitoring, which has proceeded for many years, should be studied in conjunction with what is known about toxic loadings. Similarly, little information exists regarding the significance of various attributes of habitat to survival of juvenile and young fish of various species. This lack of information leads to surprise at such discoveries as the high densities of overwintering young-of-the-year striped bass found at abandoned piers adjacent to Manhattan Island.

In the review of environmental impact assessments, it was clear that numerical models became less used with time and courtroom experience. Unfortunately, modelling efforts in the Hudson River assessments became centerpieces of legal controversies. This was a clearly inappropriate use of those models, which were found to be difficult, if not impossible, to validate. However, models can help to identify research and data-gathering needs, suggesting experiments, and providing a test of hypotheses, consequence analyses, and scenario development. Models are essential components of ongoing research programs, but they should be recognized for their shortcomings as well as for what they can help to elucidate.

Long-term monitoring of climatological and process parameters would be invaluable, as the climate of the Hudson Basin appears to be controlled by fluctuating factors of a more-or-less periodic nature. Funding for long-term research must be made available, as needed studies cannot always be fit into the constraints of 1 or 2-yr grants. The Hudson River area is fortunate in having a special foundation (Hudson River Foundation, Inc.) that funds approximately $1,000,000 is research and educational programs per year. As evidenced at local conferences and meetings, as well as in recent legislation, there is a renewed interest in grasping the dynamics of the Hudson ecosystem and in providing a model for the management of estuaries.

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References

Abood, K.A., E.A. Maikish, and R.R. Kimmel. 1976. Field and analytical investigations of ambient temperature distribution in the Hudson River, Paper 6. *In* Hudson River Ecology, 4th Symp. Hudson River Environ. Soc., Bronx, NY.

Alpine Geophysical Associates. 1974. West Side Highway Project technical report on water quality. Part II. Water quality sampling program, biological populations and inshore area studies.

Apicella. G.A., and T.F. Zimmie. 1978. Sediment and PCB transport model of the Hudson River, p. 645-653. *In* Proc. 26th Ann. Hydraulics Div. Specialty Conf., ASCE. University of Maryland, College Park, MD.

Ayres, R.U., L.W. Ayres, J. McCurley, M. Small, J.A. Tarr, and R.C. Widgery. 1985. An historical reconstruction of major pollutant levels in the Hudson–Raritan Basin 1880–1980. Variflex Corp., Pittsburgh, PA.

Ayres, R.U., and S.R. Rod. 1986. Patterns of pollution in the Hudson–Raritan basin. Environment 28(4): 14–43.

Barnthouse, L.W., J. Boreman, S.W. Christensen, C.P. Goodyear, W. Van Winkle, and D.S. Vaughan. 1984. Population biology in the courtroom: the Huson River controversy. BioScience 34(1): 14–19.

Barnthouse, L.W., R.J. Klauda, and D.S. Vaughan. 1988a. What we didn't learn about the Hudson River, why, and what it means for environmental assessment in the 1980s. *In* L.W. Barnthouse, R.J. Klauda, D.S. Vaughan, and R.L. Kendall [ed.]. Science, law, and Hudson River power plants: a case study in environmental impact assessment. Am. Fish. Soc. Monogr. 4.

Barnthouse, L.W., R.J. Klauda, D.S. Vaughan, and R.L. Kendall [ed.]. 1988b. Science, law, and Hudson River power plants: a case study in environmental impact assessment. Am. Fish. Soc. Monogr. 4.

Belton, T., B. Ruppel, K. Lockwood, S. Shiboski, G. Bukowski, R. Roundy, N. Weinstein, D. Wilson, and H. Whelan. 1985. A study of toxic hazards to urban recreational fishermen and crabbers. Office of Science and Research, NJ Department of Environmental Protection, Trenton, NJ. 68 p.

Bopp, R.I., H.J. Simpson, C.R. Olsen, and N. Kostyk. 1981. Polychlorinated biphenyls in sediments of the tidal Hudson River, New York. Environ. Sci. Tech. 15(2): 210–216.

Boreman, J. 1981. Life histories of seven fish species that inhabit the Hudson River estuary. Laboratory Reference Document No. 81-34. National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole, MA. 97 p.

Brandt, R.E. 1981. Development and management of Hudson Estuary fish resources. NY State Department of Environmental Conservation, Region 3, New Paltz, NY. (mss.)

1985. Shad and river herring in New York State: an overview. Prepared for Atlantic States Marine Fisheries Commission, Alosid Scientific and Statistical Committee. NY State Department of Environmental Conservation, Region 3, New Paltz, NY. (mss.)

Brosnan, T.M., T.L. Stokes, Jr., and A.B. Forndran. 1987. Water quality monitoring and trends in New York Harbor. Oceans '87. Marine Technology Society, Washington, DC.

Burdick, G.E. 1954. An analysis of factors, including pollution, having possible influence on the abundance of shad in the Hudson River. N.Y. Fish and Game J. 1(2): 188–205.

Busby, M.W. 1966. Flow quality and salinity profiles in the Hudson River estuary, p. 135–146. *In* Hudson River Ecology, 1st Symp. Hudson River Valley Commission, NY.

Busby, M.W., and K.I. Darmer. 1970. A look at the Hudson estuary. Water Resources Bull. 6: 802–812.

Cadee, G.C., and J. Hegeman. 1974. Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. Neth. J. Sea Res. 8: 260–291.

Central Hudson Gas and Electric. 1977. Roseton Generating Station: near-field effects of once-through cooling system operation on Hudson River biota. Central Hudson Gas and Electric Corp., Poughkeepsie, NY.

Chadwick, H.K., D.E. Stevens, and L.W. Miller. 1977. Some factors regulating the striped bass population in the Sacramento-San Joaquin estuary, California, p. 18–35. *In* W. Van Winkle [ed.] Proceedings of the conference on assessing the effects of power-plant-induced mortality on fish populations. Pergamon Press, NY.

Christensen, S.W., W. Van Winkle, L.W. Barnthouse, and D.S. Vaughan. 1981. Science and the Law: confluence and conflict on the Hudson River. Environ. Impact Assess. Rev. 2: 63-88.

COE and FHWA 1984 a,b. Supplemental environmental impact statement, Westside Highway project. Prepared jointly by U.S. Army Corps of Engineers, New York District, and by U.S. Dept. of Transportation, Federal Highway Administration, Region 1. a) Draft, May 1984 b) Final, November 1984. (Two volumes)

Crecco, V.A., and T.F. Savoy. 1985. Effects of biotic and abiotic factors on growth and relative survival of young American shad, *Alosa sapidissima*, in the Connecticut River. Can. J. Fish. Aquat. Sci. 42: 1640-1648.

Darmer, K.I. 1969. Hydrologic characteristics of the Hudson River estuary, p. 40-45. *In* G.P. Howells and G.J. Lauer [ed.] 2nd Hudson River ecology symposium, Tuxedo, NY. N.Y.S. Dept. of Environmental Conservation, Albany, NY.

Deck, B.L. 1981. Nutrient-element distributions in the Hudson estuary. Ph. D. dissertation. Columbia Univ., New York, NY. 396 p.

Dey, W., T. Peck, C. Smith, S. Cormier, and G. Kreamer. 1986. A study of the occurrence of liver cancer in Atlantic tomcod from the Hudson River Estuary. Final Report to Hudson River Foundation. HRF 016/83B. Hudson River Foundation, New York. 51 p.

EA. 1981. Bowline Point Generating Station entrainment abundance and survival studies. 1979 annual report with overview of 1975-1979 studies. Prepared by Ecological Analysts, Inc. for Orange and Rockland Utilities, Inc.

FHWA. 1977. West-Side highway project. Final environmental impact statement. U.S. Dept. of Transportation. 300+p.

Findlay, S., M. Pace, and D. Lints. 1988. Bacterial biomass and production in the tidal freshwater Hudson River. EOS 69(44): 1135 (abstract).

Fleming, A., K.A. Abood, H.F. Mulligan, C.B. Dew, C.A. Menzie, W. Sydor, and W. Su. 1976. The environmental impact of PL 92-500 on the Hudson River estuary, Paper 16. *In* Hudson River Ecology, 4th Symp. Hudson River Environ. Soc., Bronx, NY.

Fletcher, R.I. 1981. Affidavit of R. Ian Fletcher. U.S. District Court, Southern District of New York. 81 Civ. 3000 (TPG).

Fruci, J., and R. W. Howarth. 1988. Carbon nitrogen, and phosphorus inputs to the tidal freshwater portion of the Hudson River estuary from point and nonpoint sources. Final Report to the Ecosystems Research Center, Cornell University, Ithaca, NY. ERC-183.

FWS 1985. Emergency Striped Bass Research Study. 1984 annual report. Prepared jointly by the U.S. Fish and Wildlife Service and the National Marine Fisheries Service. (mss.)

Garritt, R., R. Marino, J. Fruci, and R. Howarth. 1988. Whole-system metabolism of the tidal freshwater portion of the Hudson River Estuary. EOS 69(44): 1136 (abstract).

Garside, C., T.C. Malone, O.A. Roels, and B.A. Sharstein. 1976. An evaluation of sewage derived nutrients and their influence on the Hudson estuary and New York bight. Estuarine Coastal Mar. Sci. 4: 281-289.

Gladden, J.B., F.C. Cantelmo, J.M. Croom, and R. Shapot. 1988. An evaluation of the Hudson River ecosystem in relation to the dynamics of fish populations. *In* L.W. Barnthouse, F.J. Klauda, D.S. Vaughan, and R.L. Kendall [ed.] Science, law, and Hudson River power plants: a case study in environmental impact assessment. Am. Fish. Soc. Monogr. 4.

Heffner, R.L. 1973. Phytoplankton community dynamics in the Hudson River estuary between mile points 38 and 77, Paper 17. *In* Hudson River Ecology, 3rd Symp. Hudson River Environmental Society, Bear Mountain, NY.

Helsinger, M.H., and G.M. Friedman. 1982. Distribution and incorporation of trace elements in the bottom sediments of the Hudson River and its tributaries. Northeastern Environ. Sci. (1): 33-47.

Hetling, L. 1976. Trends in wastewater loading, 1900-1976, Paper 14. *In* Hudson River Ecology, 4th Symp. Hudson River Environmental Society. Bronx, NY.

Hetling, L., E. Horn, and J. Tofflemire. 1978. Summary of Hudson River PCB study results. Technical Paper 51, NYS Department of Environmental Conservation, Albany, NY. 88 p.

Horn, E.G., L.J. Hetling, and T.J. Tofflemire. 1979. The problem of PCBs in the Hudson River system. Ann. N.Y. Acad. Sci. 320: 591-609.

Horn, E.G. and L.C. Skinner. 1985. Final environmental impact statement for policy on contaminants in fish for N.Y.S. Department of Environmental Conservation, Division of Fish and Wildlife, Albany, NY. 150 p.

Horne, W.S. 1979. Hudson River basin. Level B: water and related land resources study. Technical Paper 3. NY State Department of Environmental Conservation, Albany, NY. (3 vol.)

Howells, G.P., T.J. Kneip, and M. Eisenbud. 1970. Water quality in industrial areas: profile of a river. Environ Sci. Tech. 4: 26-35.

HRF. 1984. Proceedings of a PCB workshop held January 19, 1984. Hudson River Foundation for Science and Environmental Research, Inc. New York., NY.

1987. Hudson River Foundation 1987 Annual River Symposium, Bear Mountain, New York, N.Y.

1988. Hudson River Foundation Grants 1987-88. Hudson River Foundation, NY. 16 p.

Hudson River Policy Committee. 1968. Hudson River fisheries investigations (1965-1968). Report to Consolidated Edison Co. of New York, Inc. (2 vols)

Hydroscience. 1979. Analysis of the fate of PCB's in the ecosystem of the Hudson estuary. Prepared for NYS Department of Environmental Conservation by Hydroscience, Inc., Westwood, NY.

Kahnle, A.W., and R.E. Brandt. 1985. Biology and management of striped bass in New York waters. Final report for U.S. Dept. of Commerce, National Marine Fisheries Service Emergency Striped Bass Study. N.Y. State Department of Environmental Conservation, New Paltz, NY. 130 p.

Klauda, R.J., W.P. Dey, T.B. Hoff, J.B. McLaren, and Q.E. Ross. 1980. Biology of Hudson River juvenile striped bass, p. 101-123. *In* H. Clepper [ed.] Proc. 5th Ann. Mar. Res. Fish. Symp. Sport Fishing Institute, Washington, DC.

Klauda, R.J., M. Nittel, and K.P. Campbell. 1977. The commercial fishery for American shad in the Hudson River: fishing effort and stock abundance trends, p. 107-134. *In* Proceedings of a workshop on American shad, December 14-16, 1976, Amherst, MA. NTIS, Springfield, VA.

Klauda, R.J, T.H. Peck, and G.K. Rice. 1981. Accumulation of polychlorinated biphenyls in Atlantic tomcod (*Microgadus tomcod*) collected form the Hudson River estuary, New York. Bull. Environ. Contam. Toxocol. 27: 829-835.

Lane, G.A. 1970. An initial fisheries survey of the Hudson River from Lock No. 1 to Fort Edward. NY State Department of Environmental Conservation, Bureau of Fisheries, Albany, NY. 18 p. (mss., cited in Sheppard 1976)

Lars. 1985. International Large River Symposium: Program Update. (pamphlet)

Lauder, G.V., and K.F. Liem. 1983. The evolution and interrelationships of the actinopterygian fishes. Bull. Mus. Comp. Zool., Harvard 150: 95-197.

Lawler, J.P. 1972a. The effect of entrainment at Indian Point on the population of the Hudson River striped bass. Written testimony presented on April 5, 1972 before the U.S. Atomic Energy Commission in the matter of Consolidated Edison Co.

of New York, Inc. (Indian Point Station, Unit 2).

1972b. The effect of entrainment at Indiant Point on the population of the Hudson River striped bass. Written testimony presented on October 30, 1972 before the U.S. Atomic Safety and Licensing Board in the matter of Consolidated Edison Co. of New York, Inc. (Indian Point Station, Unit 2), USAEC Docket 50-247.

1974. Effect of entrainment and impingement at Cornwall on the Hudson River striped bass population. Testimony presented to the Federal Power Commission in the matter of Cornwall, USFPC Project No. 2338, October 1974.

LEVIN, S.A. 1979. The concept of compensatory mortality in relation to impacts of power plants on fish populations. Written testimony prepared for the U.S. Environmental Protection Agency, Region II.

LIMBURG, K.E. 1984. Environmental impact assessment of the PCB problem: a review. Northeastern Environ. Sci. 3(3/4): 124–137.

1985. The role of research in solving environmental problems: the Hudson River experience, p. 66–77. *In* L. Dworsky, P. Otis, G. Galloway, and W.J. Reynolds [ed.]. Proc. 6th Hudson River Ecology Symp. Hudson River Environmental Society, New Paltz, NY.

LIMBURG, K.E., M.A. MORAN, AND W.H. MCDOWELL. 1986a. The Hudson River ecosystem. Springer-Verlag New York, Inc. 325 p.

LIMBURG, K.E., S.A., LEVIN, AND C.C. HARWELL. 1986b. Ecology and estuarine impact assessment: lessons learned from the Hudson River (U.S.A.) and other estuarine experiences. J. Environ. Manage. 22: 255–280.

LMS. 1977a. 1976 Hudson River aquatic ecology studies at Lovett Generating Station. Vol 1. Chapters I–VII. Prepared by Lawler, Matusky and Skelly Engineers for Orange and Rockland Utilities, Inc.

1977b. Roseton Generating Station: Near-field effects of once-through cooling system operation on Hudson River biota. Prepared by Lawler, Matusky and Skelly Engineers, and by Ecological Analysts, Inc. for Central Hudson Gas and Electric Corp.

1978. Roseton and Danskammer Point Generating Stations. Hydrothermal analysis. Prepared by Lawler, Matusky and Skelly Engineers for Central Hudson Gas and Electric Corp.

1980. Biological and water quality data collected in the Hudson River near the proposed Westway project during 1979–1980. Lawler, Matusky and Skelly Engineers. Prepared for NYS Department of Transportation and System Design Concepts, Inc. 2 vols.

MALONE, T.C. 1977. Environmental regulation of phytoplankton productivity in the lower Hudson estuary. Estuarine Coastal Mar. Sci. 5: 157–171.

1984. Anthropogenic nitrogen loading and assimilation capacity of the Hudson River estuarine system, USA, p. 291–311. *In* V.S. Kennedy [ed.] The estuary as a filter. Academic Press, Orlando, FL.

MALONE, T.C., P.J. NEALE, AND D. BOARDMAN. 1980. Influences of estuarine circulation on the distribution and biomass of phytoplankton size fractions, p. 249–262. *In* V.S. Kennedy [ed.] Estuarine perspectives. Academic Press, New York, NY.

MARSHALL, N., C.A. OVIATT, AND D.M. SKAUEN. 1971. Productivity of the benthic microflora of shoal estuarine environments in southern New England. Int. Rev. der Ges. Hydrobiol. 56: 947–956.

MCFADDEN, J.T., AND J.P. LAWLER [ed.]. 1977. Supplement I to: Influence of Indian Point Unit 2 and other steam electric generating plants on the Hudson River estuary with emphasis on striped bass and other fish populations. Prepared for Consolidated Edison Co. of New York, Inc.

MCFADDEN, J.T., TEXAS INSTRUMENTS, INC., AND LAWLER, MATUSKY AND SKELLY, ENGINEERS. 1977. Influence of Indian Point Unit 2 and other steam electric generating plants on the Hudson River Estuary, with emphasis on striped bass and other fish populations. Prepared for Consolidated Edison Co. of New York, Inc.

1978. Influence of the proposed Cornwall pumped storage project and steam electric generating plants on the Hudson River Estuary, with emphasis on striped bass and other fish populations. Revised. Prepared for Consolidated Edison Co. of New York, Inc.

MIHURSKY, J.A., W.R. BOYNTON, E.M. SETZLER-HAMILTON, AND K.U. WOOD. 1981. Freshwater influences on striped bass population dynamics, p. 149–167. *In* Proc. Natl. Symp. on Freshwater Inflow to Estuaries. U.S. Fish and Wildlife Service. FWS/OBS-81/04.

MOORE, E. 1937. Introduction, p. 9–19. *In* A biological survey of the lower Hudson watershed. Suppl. 26th Ann. Report, 1936. N.Y. State Conservation Department Albany, NY.

NADEAU, R.J., AND R. DAVIS. 1974. Investigation of polychlorinated biphenyls in the Hudson River: Hudson Falls-Fort Edward area. EPA Region II report.

NOAA. 1982. Monthly normals of temperature, precipitation, and heating and cooling degree days, 1951-1980. New York. Climatography of the United Stated No. 81. U.S. Dept. of Commerce, National Oceanic and Atmospheric Administration, Environmental Data and Information Service, National Climatic Center. Asheville, NC. 18 p.

NYS CONSERVATION DEPT. 1933. A biological survey of the upper Hudson watershed. Suppl. 22nd Ann. Report, 1932. N.Y. State Conservation Department, Albany, NY. 373 p.

1937. A biological survey of the lower Hudson watershed. Suppl. 26th Ann. Report, 1936. N.Y. State Conservation Department, Albany, NY. 373 p.

NYSDEC. 1976. Settlement agreement between Department of Environmental Conservation and General Electric Company, in the matter of alleged violations of § 17-0501, 17-0511 and 11-0503 of the Environmental Conservation Law of the State of New York by General Electric Company, Respondent. File No. 2833.

NEW YORK STATE ECONOMIC DEVELOPMENT BOARD. 1975. Economic impact of regulating the use of PCB's in New York State. Prepared by Economic Development Board staff. Albany, NY. 28 p. (mss.)

NYU. 1976, 1978. Hudson River ecosystem studies. Effects of entrainment by the Indian Point Power plant on biota in the Hudson River estuary. Prepared by the Institute of Environmental Medicine, New York University Medical Center, for Consolidated Edison Co. of New York, Inc.

OCEANIC SOCIETY. 1980. Hudson River fishery management program study. A report to the New York State Department of Environmental Conservation in satisfaction of tasks mandated by Section 11-0306 of the Environmental Conservation Law. The Oceanic Society, Stamford, CT.

ODUM, E.P. 1971. Fundamentals of ecology, 3rd Ed. W.B. Saunders Co., Philadelphia, PA. 574 p.

O'REILLY, J.E., J.P. THOMAS, AND C. EVANS. 1976. Annual primary production (nannoplankton, netplankton, dissolved organic matter) in the lower New York Bay. Paper 19. *In* Hudson River Ecology, 4th Symp. Hudson River Environmental Soc., Bronx, NY.

PACE, M.L., S.F. FINDLAY, AND D. L. LINTS. 1988. Variability in Hudson River zooplankton: similarities and differences with open water. EOS 69(44): 1136 (abstract).

PEARCE, J.B., D.J. RADOSH, J.V. CARRACCIOLO, AND F.W. STEIMLE, JR. 1981. Benthic Fauna. MESA New York Bight Atlas Monograph 14. N.Y. Sea Grant Institute, Albany, NY. 79 p.

PEIERLS, B., N.F. CARACO, AND J.J. COLE. 1988. Primary productivity in the Hudson River. EOS 69(44): 1135 (abstract).

RISTICH, S.S., M. CRANDALL, AND J. FORTIER. 1977. Benthic and epibenthic macroinvertebrates of the Hudson River. I. Distribution, natural history and community structure. Estuarine. Coastal Mar. Sci. 5: 255–266.

ROHMANN, S.O., R.L. MILLER, E.A. SCOTT, AND W.R. MUIR. 1985. Tracing a river's toxic pollution: a case study of the Hudson. INFORM, Inc. New York. 154 p.

SANDERS, J.E. 1982. The PCB-pollution problem of the upper Hudson River from the perspective of the Hudson River PCB Settlement Advisory Committee. Northeastern Environ. Sci. 1(1): 7–18.

SANDLER, R., AND D. SCHOENBROD. 1981. The Hudson River power plant settlement. Materials prepared for a conference. New York University, New York, NY.

SCHMIDT, R.E., R.J. KLAUDA, AND J.M. BARTELS. 1988. Distributions and movements of the early life stages of three *Alosa* spp. in the Hudson River estuary, with comments on the evidence for mechanisms that may reduce interspecific competition. *In* L.W. Barnthouse, R.J. Klauda, D.S. Vaughan, and R.L. Kendall [ed.] Science, law, and Hudson River power plants: a case study in environmental impact assessment. Amer. Fish. Soc. Monogr. 4.

SCHROEDER, R.A. AND C.R. BARNES. 1983. Trends in polychlorinated biphenyl concentrations in Hudson River water five years after elimination of point sources. U.S. Geological Survey. Water-Resources Investigations Report 83-4206. Albany, NY. 28 p.

SERI. 1981. Solar radiation energy resource atlas of the United States. SERI/SP-642-1037. Solar Energy Research Inst., Golden, CO.

SHEPPARD, J.D. 1976. Valuation of the Hudson River fishery resources: past, present and future. Technical Report. N.Y. State Department of Environmental Conservation, Bureau of Fisheries, Albany, NY. 50 p.

1983. Valuation of Hudson River fisheries. Appendix B: Commercial fisheries. Appendix C: Recreational fisheries. N.Y. State Department of Environmental Conservation, Bureau of Environmental Protection, Albany, NY. (mss).

SIMPSON, H.J., R. BOPP, AND D. THURBER. 1974. Salt movement patterns in the Hudson, Paper 9. *In* Hudson River Ecology, 3rd Symp. Hudson River Environmental Society, Bear Mountain, NY.

SIROIS, D.L., AND S.W. FREDRICK. 1978. Phytoplankton and primary productivity in the lower Hudson River estuary. Estuarine Coastal Mar. Sci. 7: 413–423.

SLOAN, R., E.G. HORN, B. YOUNG, C.ZAWACKI, AND A. FORTI. 1986. PCB in striped bass from the marine district of New York. Technical Report 86-1 (BEP). NY State Department of Environmental Conservation, Albany, NY.

SLOBODKIN, L.J. 1979. Critique of the utilities' striped bass density-dependence arguments and research policy and programs. Written testimony prepared for the New York State and Massachusetts Attorneys General.

SMITH, C.E., T.H. PECK, R.J. KLAUDA, AND J.B. MCLAREN. 1979. Hepatomas in Atlantic tomcod *Microgadus tomcod* (Waldbaum) collected in the Hudson River estuary in New York. J. Fish Diseases d2: 313–319.

SMITH, C.L. [ed.]. 1987. Fisheries research in the Hudson River. State University of New York Press, Albany, NY. 368 p.

STEDFAST, D.A. 1982. Flow model of the Hudson River estuary from Albany to New Hamburg, NY. U.S. Geological Survey. Water-Resources Investigations Report 81-55. Albany, NY. 69 p.

SWARTZMAN, G.L, R.B. DERISO, AND C. COWAN. 1978. Comparison of simulation models used in assessing the effects of power-plant-induced mortality on fish populations. UW-NRC-10. Center for Quantitative Science, College of Fisheries, Univ. of Washington, Seattle, WA.

TALBOT, G.B. 1954. Factors associated with fluctuations in abundance of Hudson River shad. U.S. Fish and Wildlife Bull. 101(56): 373–413.

TALBOT, A.R. 1983. Settling things: six case studies in environmental mediation. The Conservation Foundation, Washington, DC. 101 p.

TEXAS INSTRUMENTS. 1974, 1975. Hudson River ecological study in the area of Indian Point. Annual reports for 1973 and 1974. Prepared by Texas Instruments, Inc. for Consolidated Edison Co. of New York, Inc.

TEXAS INSTRUMENTS. 1976. Hudson River ecological study in the area of Indian Point. Thermal effects report. Prepared by Texas Instruments, Inc. for Consolidated Edison Co. of New York, Inc.

1979. 1978 water quality data display. Prepared by Texas Instruments, Inc. for Consolidated Edison Co. of New York, Inc.

1981. 1979 year class report for the multiplant impact study of the Hudson River estuary. Prepared by Texas Instruments, Inc. for Consolidated Edison Co. of New York, Inc.

THOMAS, J.P., W. PHOEL, J.E. O'REILLY, AND C. EVANS. 1976. Seabed oxygen consumption in the lower Hudson estuary. National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Sandy Hook Lab, Highlands, NJ. 21 p.

TOFFLEMIRE, T.J., AND S.O. QUINN. 1979. PCB in the upper Hudson River: mapping and sediment relationships. Technical Paper No. 56. NY State Department of Environmental Conservation, Albany, NY. 140 p.

USGS. 1969. Water resources data for New York. Water year 1980. U.S. Geological Survey Water Data Report NY-80-1. 310 p.

WEINSTEIN, L.H. [ed.]. 1977. An Atlas of the Biologic Resources of the Hudson Estuary. Boyce Thompson Institute for Plant Research, Inc. Yonkers, NY. 104 p.

WOODHEAD, P.M.J. 1987. The fish community of New York Harbor, and spatial and temporal distributions of major species. Paper presented at Conference on the impacts of New York Harbor development on aquatic resources, October 28–29. Hudson River Foundation, New York, NY.

Fish Production in Two Large Atlantic Coast Rivers: Miramichi and Exploits

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Abstract

RANDALL, R. G., M. F. O'CONNELL, AND E. M. P. CHADWICK. 1989. Fish production in two large Atlantic coast rivers: Miramichi and Exploits, p. 292–308. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The Miramichi River, New Brunswick, and the Exploits River, Newfoundland, have roughly similar watershed areas (about 13 000 km^2), discharge rates (annual means of 300 $m^3 \cdot s^{-1}$) and water chemistry, but their fish communities and fisheries are quite different. Miramichi River is inhabited by 30 species of fish while Exploits has 5; however, anadromous Atlantic salmon (*Salmo salar*) is the most important species, in terms of both riverine biomass and economic importance, in both rivers. Fish production in fluvial habitat is estimated to be low, about 4 to 6 $g \cdot m^{-2} \cdot yr^{-1}$ in both rivers. Despite low freshwater productivities, however, fisheries yield is relatively high because of the contributions of anadromous species, for which most biomass is produced in the marine environment. In Miramichi River, fish landings have averaged 550 $kg \cdot ha^{-1} \cdot yr^{-1}$, while landings from Exploits River are considerably less (40 $kg \cdot ha^{-1} \cdot yr^{-1}$) because of the fewer anadromous species in this river. Major stresses on these fisheries have included pollution from mining and forest-based industries (both rivers), impoundments (Exploits) and overfishing (Miramichi). Enhancement projects on the Exploits River have increased fish production by introducing salmon into areas previously inaccessible to them.

Résumé

RANDALL, R. G., M. F. O'CONNELL, AND E. M. P. CHADWICK. 1989. Fish production in two large Atlantic coast rivers: Miramichi and Exploits, p. 292–308. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

La rivière Miramichi, au Nouveau-Brunswick, et la rivière Exploits, à Terre-Neuve, sont caractérisées par des bassins hydrographiques de superficie presque identique (environ 13 000 km^2), un débit similaire (moyenne annuelle de 300 $m^3 \cdot s^{-1}$) et une composition chimique de l'eau semblable, mais les communautés de poissons et la pêche sont assez différentes. La rivière Miramichi est fréquentée par 30 espèces de poissons comparativement à 5 pour la rivière Exploits; toutefois, le saumon atlantique anadrome (*Salmo salar*) est l'espèce la plus importante en termes de biomasse riveraine et d'importance économique dans les deux cours d'eau. Selon les estimations, la production de poisson dans l'habitat fluvial est faible, soit de 4 à 6 $g \cdot m^{-2} \cdot an^{-1}$ dans les deux dours d'eau. Malgré une faible productivité en eau douce, le rendement de pêche est assez élevé en raison de la présence d'espèces anadromes dont la biomasses est produite engrande partie en mer. Les débarquements s'élèvent en moyenne à 550 $kg \cdot ha^{-1} \cdot an^{-1}$ dans la rivière Miramichi, mais ils sont beaucoup plus faibles (40 $kg \cdot ha^{-1} \cdot an^{-1}$) dans la rivière Exploits où les espèces anadromes sont moins nombreuses. La pollution causée par l'industrie minière et forestière (dans les deux cours d'eau), la construction d'ouvrages de retenue (rivière Exploits) et de la surpêche (rivière Miramichi) représentent les principales contraintes. Les projets de mise valeur dans la rivière des Exploits ont permis d'accroître la production de poissons grâce à l'introduction du saumon dans des zones autrefois inaccessibles.

1. Introduction

The primary purpose of this paper is to compare fish production and yield in two large rivers on Canada's Atlantic coast, the Miramichi River, New Brunswick, and the Exploits River, Newfoundland. These rivers are interesting to compare because although they have roughly similar watershed areas, discharge rates and water chemistry, and are dominated in terms of riverine biomass and economic importance by Atlantic salmon (*Salmo salar*) populations,

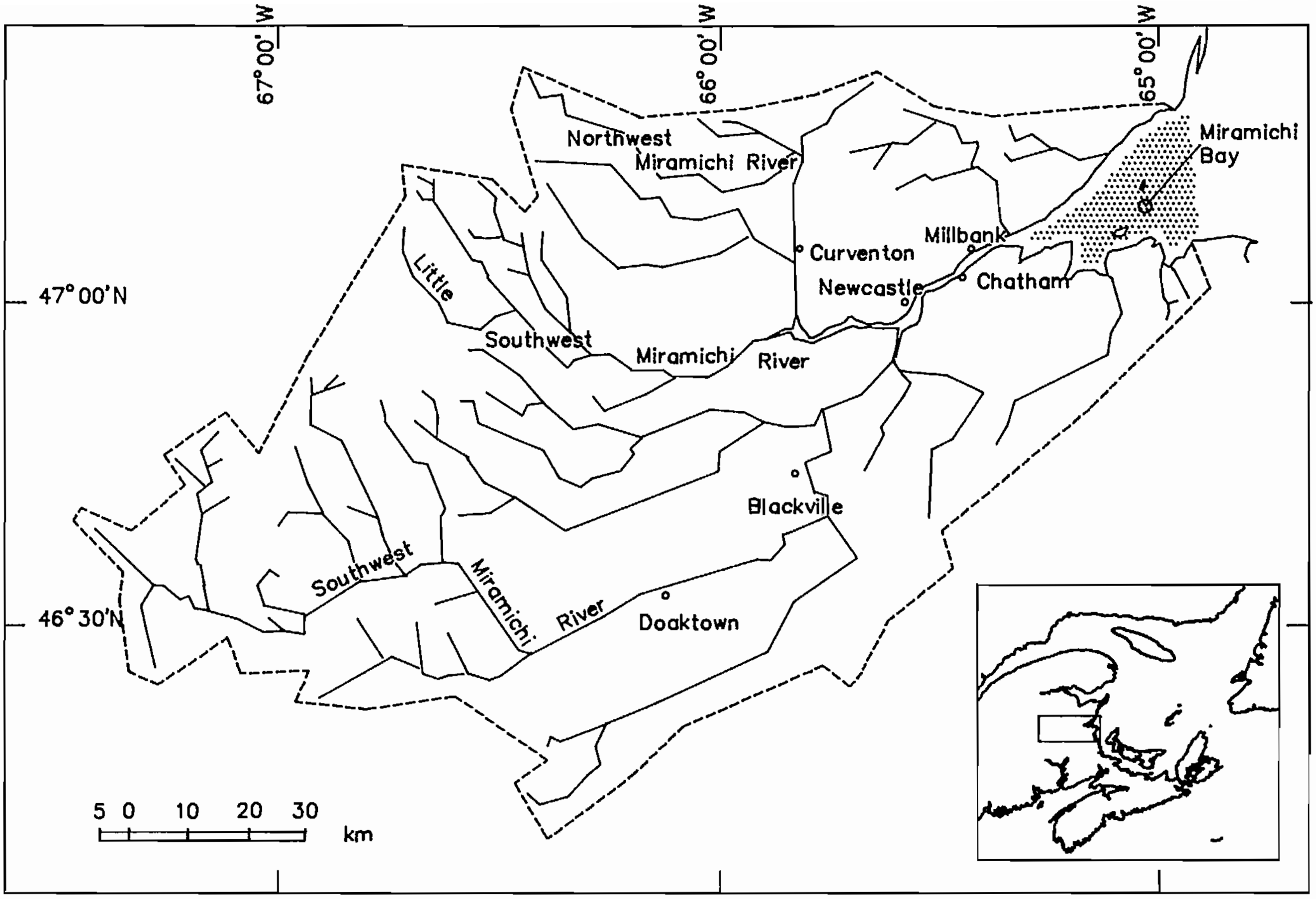

FIG 1. The Miramichi watershed and its location in eastern Canada.

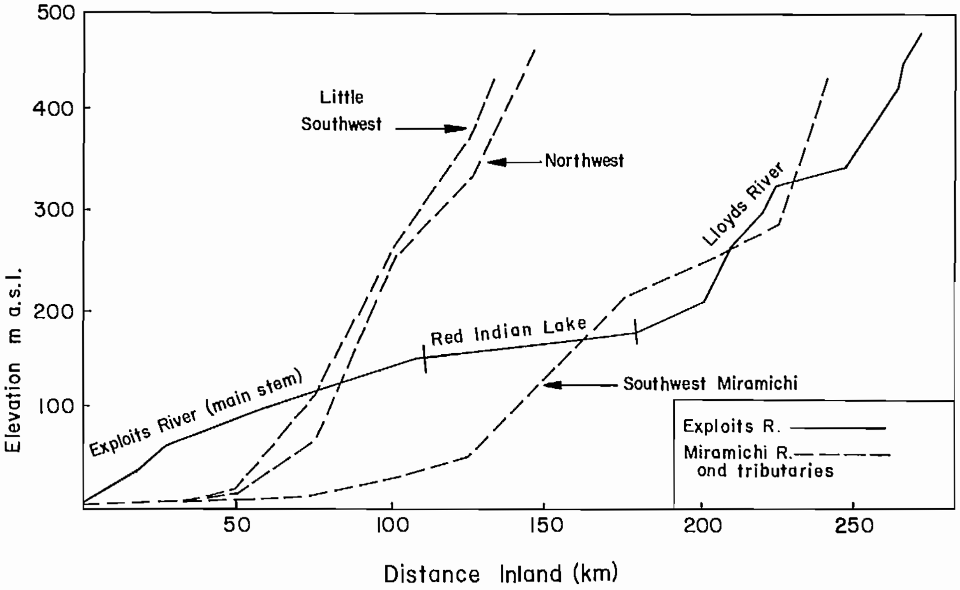

FIG 2. Relief profiles of the Miramichi and Exploits rivers.

they are very dissimilar in other ways. For example, Miramichi River has few lakes, its watershed is completely accessible to anadromous fish and it has 30 native fish species. By contrast, Exploits River has extensive lacustrine habitat, is relatively inaccessible to migrating fish and has only 5 native fish species. Both watersheds have been sig-

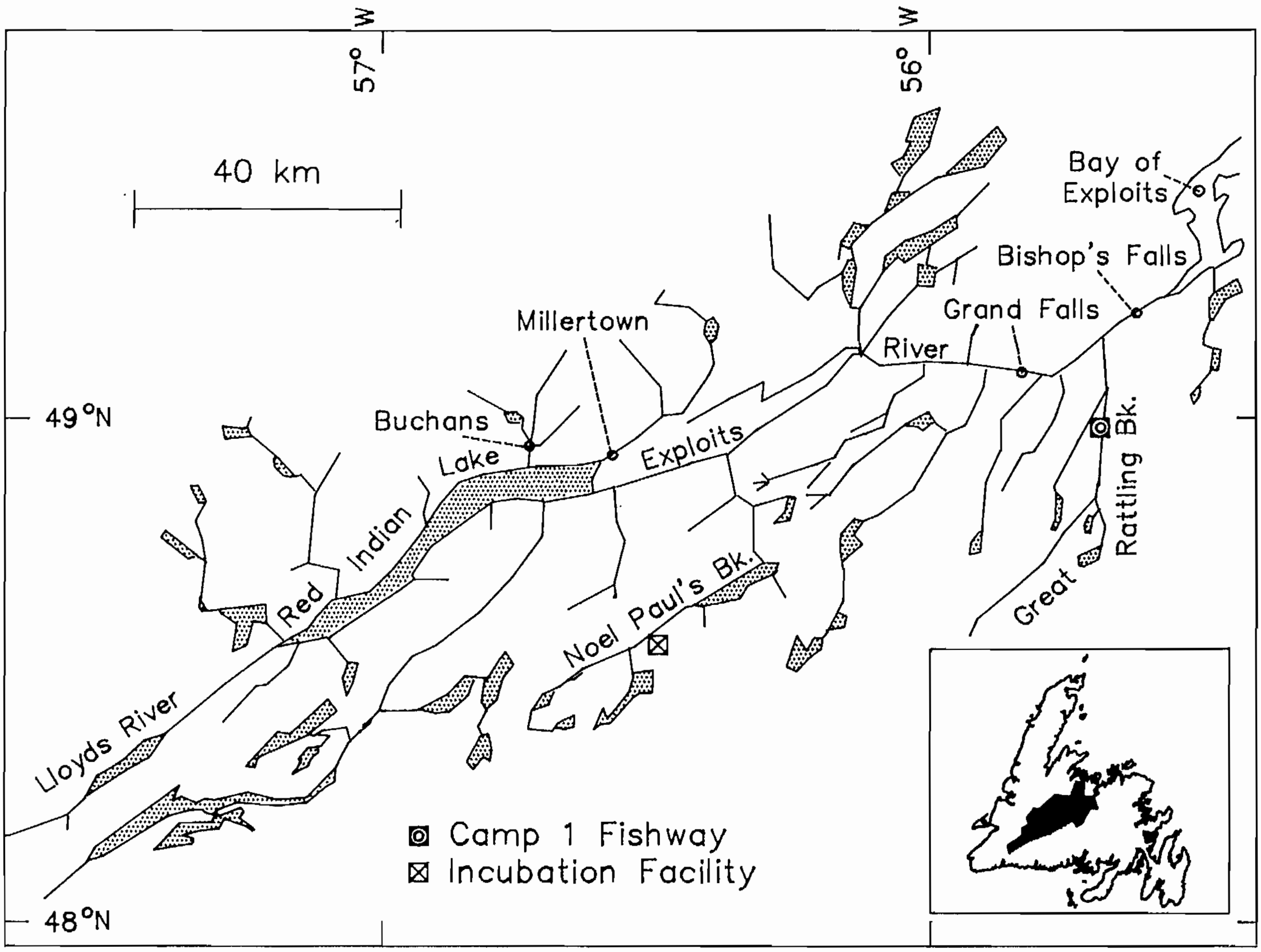

FIG 3. The Exploits watershed. Inset shows the location of the watershed in insular Newfoundland.

nificantly affected by man because of extensive forest-based industry and in Exploits River by hydroelectric development.

A secondary objective of this paper is to highlight the importance of anadromous fishes in these rivers. Although freshwater productivity is apparently low, fisheries yield is relatively high because of the presence of anadromous species, particularly in the Miramichi River.

2. Description of Watersheds

The Miramichi and Exploits rivers are similar in size. The Miramichi watershed, the second largest in New Brunswick, is elliptical in shape, covering about 14 000 km^2 in area (Table 1, Fig. 1). Two major tributaries are the Northwest Miramichi (area about 3 900 km^2) and the Southwest Miramichi (about 7 700 km^2). Maximum headwater elevation occurs in the upper Northwest Miramichi at about 470 m above sea level (Fig. 2) and average gradient along the axial length of the major tributary is about 2.3 m•km^{-1}. Amiro (1983) estimated that the total fluvial habitat area above head of tide is 55 × 10^6 m^2.

The Exploits watershed (Fig. 3) is the largest in insular Newfoundland with a drainage area of about 11 300 km^2 (Table 1). Maximum relief is 490 m above sea level in the headwaters of the Lloyds River tributary and average gradient is about 1.8 m•km^{-1}. Fluvial habitat area has been estimated to be about 52 × 10^6 m^2. Unlike the Miramichi River, the Exploits has numerous headwater lakes; total lacustrine habitat is about 866 × 10^6 m^2 (Table 1). About 49 % of these lakes are <10 ha, 34 % are 11–50 ha and 17 % are >50 ha. Red Indian Lake (Fig. 3) is the second largest lake in Newfoundland with an area of 18 121 ha.

Geology, soils and forest cover are similar for the two watersheds. Headwaters of the Miramichi basin are underlain by Ordovician, Silurian and Devonian aged bedrocks, including granite, quartz, monzonite, granodiorite and related rocks. The Maritime Plain areas of the southeast basin are underlain by conglomerates, sandstones and siltstones of Pennsylvanian or younger age. Most of the drainage basin is covered by glacial till moraine deposits. Soils vary from humo-ferric podzol (peaty) along the shore and over most of the basin to grey luvisol in the southwest. The entire watershed is wooded by tree species typical of the Acadia forest region (Hosie 1969): mixed forests of *Picea* *rubens*, *Abies balsamea*, *Tsuga canadensis*, *Pinus strobus*, *Acer saccharum*, and *Betula alleghaniensis*. Most of the Miramichi forest has been logged during the last two centuries.

Bedrock geology of the major part of the Exploits basin is Ordovician acidic to mafic volcanic rocks with associated slate, greywacke, siltstone, sandstone and conglomerates. Smaller areas of Silurian and Devonian sedimentary igneous and volcanic rocks also occur (e.g. west of Red Indian Lake). Soils are similar to the headwaters of the Miramichi, primarily humo-ferric podzols. The Exploits watershed, like the rest of insular Newfoundland, is covered with boreal coniferous forest, dominated by *Abies balsamea* and *Picea mariana*, with occasional small stands of *Betula papyrifera* and *Picea glauca*.

Average annual discharge is approximately 320 $m^3 \cdot s^{-1}$ for Miramichi and 290 $m^3 \cdot s^{-1}$ for Exploits rivers (Anonymous 1985). Total annual precipitation averages about 1 000 mm in both the Miramichi and Exploits watersheds, and it is distributed relatively uniformly throughout the year. Because of snow melt, however, peak river discharge occurs April to June and another minor peak occurs October to November (Fig. 4).

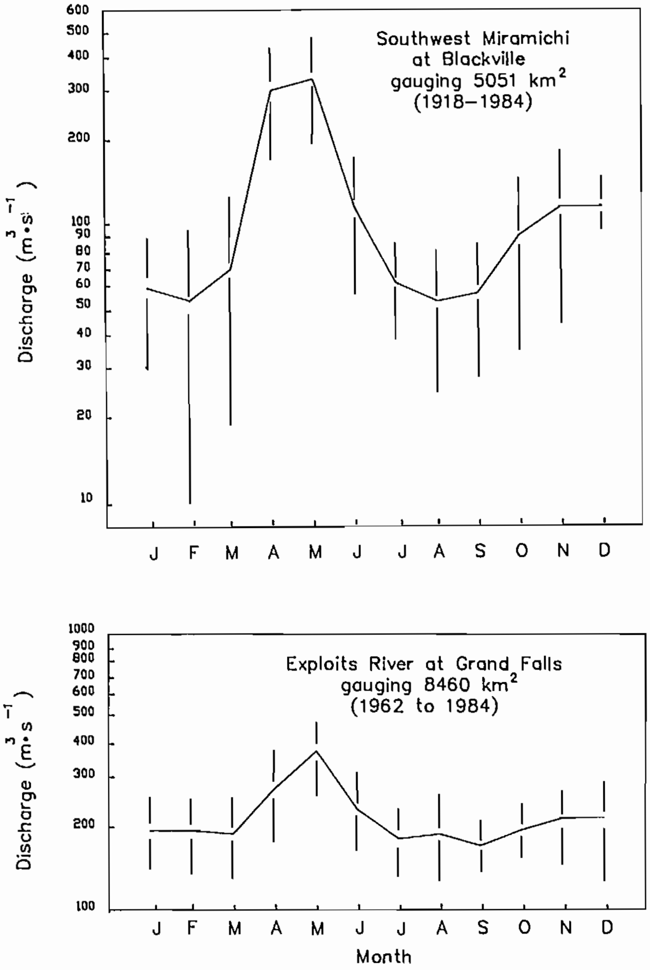

FIG 4. Mean monthly discharge (± SD) for the Miramichi River at Blackville and the Exploits River at Grand Falls. Data from Anonymous 1985.

TABLE 1. Physical characteristics of the Miramichi and Exploits watersheds.

	River	
	Miramichi	Exploits
Watershed area (km^2)	13 799	11 272
Maximum elevation (m)	470	488
Average slope ($m \cdot km^{-1}$)	2.3	1.8
Rearing area (m^2)		
Fluvial	55×10^6	52×10^6
Lacustrine	Negligible	866×10^6
Stream order (mouth)	7	6
Growing season		
Degree-days >5.6°C	2 000–2 500	1 500–2 000
Days	170– 190	160– 170
Frost-free season (days)	100– 200	80– 100
Lakes frozen (days)	125– 155	155– 185
Precipitation (total mm)	1 098	991

Chemical analyses of water from the Miramichi and Exploits rivers have been conducted periodically by Environment Canada since 1965 (Anonymous 1979, 1982). Average conductivity in both rivers is low (28–49 $\mu S \cdot cm^{-1}$), as are concentrations of nutrient elements and major cations and anions (Table 2). There is some evidence that the Miramichi River has a slightly higher conductivity than the Exploits River. Surveys of eight headwater tributaries in the Exploits River indicated average conductivities ranged between 20 and 35 $\mu S \cdot cm^{-1}$ (D.A. Scruton, Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, Science Branch, P.O. Box 5667, St. John's, Nfld. A1C 5K1, unpublished data) while 11 headwater tributaries on the Miramichi ranged between 34 and 363 $\mu S \cdot cm^{-1}$ (Anonymous 1982).

Urban development has largely been restricted to the lower watershed in both rivers. Seven communities are located on the Exploits watershed; Grand Falls is the largest (population of 17 500) while remaining towns range from 4 400 (Bishop's Falls) to 230 (Millertown) people (Fig. 3). Chatham and Newcastle (combined populations of 14 000), located on the estuary, are the largest communities on the Miramichi River, while other smaller towns are located further up river (Fig. 1). Most headwater reaches in both rivers, however, are relatively unpopulated. Pulp and paper operations are the major employers on both rivers.

Eleven diadromous and 19 freshwater species of fish have been recorded from the Miramichi River (Table 3, McKenzie 1959; Scott and Crossman 1973). Of these, 10 species are harvested by commercial and recreational fishermen. In contrast, only 3 diadromous and 2 freshwater species inhabit the Exploits River (Table 3), reflecting the general scarcity of fish species found in freshwaters of insular Newfoundland (Scott and Crossman 1964); three of the 5 species are harvested.

3. Description of Fisheries

3.1 Miramichi River

Historically, Atlantic salmon were commercially exploited by trap net and drift net fishermen in Miramichi

TABLE 2. Chemical analyses of water samples from the Miramichi and Exploits rivers. Values are means (standard deviations in parentheses) except for pH, which are medians (ranges in parentheses). Units are mg•L^{-1}, except where otherwise indicated. Data from Anonymous (1979, 1982).

	Miramichi		Exploits	
	Northwest (Redbank)	Southwest (Blackville)	Grand Falls	Bishops Falls
Conductivity (μS•cm^{-1})	49.0(14.0)	41.0(15.0)	28.0(35.0)	39.0(27.0)
Turbidity (JTU)	1.3(1.7)	1.7(4.3)	1.0(0.9)	3.0(5.0)
Colour (rel. units)	29.0(19.0)	35.0(17.0)	30.0(12.0)	30.0(11.0)
pH	6.8(5.9–7.7)	6.8(3.9–7.8)	6.5(4.1–8.2)	6.2(4.2–7.2)
Total alkalinity ($CaCO_3$)	11.0(4.0)	10.9(6.7)	4.8(1.9)	6.2(12.6)
Total dissolved solids	26.0(7.0)	22.0(9.0)	13.0(2.0)	19.0(14.0)
Total hardness ($CaCO_3$)	18.7(6.3)	15.2(5.8)	7.7(1.1)	—
Anions				
Chloride	1.9(1.9)	1.9(0.8)	2.2(0.4)	3.2(1.7)
Sulphate	8.7(2.9)	6.5(4.7)	3.5(4.9)	4.9(1.9)
Cations				
Calcium	6.1(2.0)	4.8(2.3)	2.4(0.4)	3.1(1.9)
Potassium	0.5(0.2)	0.4(0.2)	0.2(0.1)	0.4(0.2)
Sodium	1.9(1.2)	2.2(0.8)	1.5(0.7)	2.5(0.9)
Nutrient elements				
Carbon — total inorganic	2.5(0.4)	1.9(0.9)	1.7(0.8)	—
total organic	8.0(5.5)	7.6(2.9)	10.5(4.8)	9.7(2.7)
Nitrogen — NO_3 and NO_2	0.061(0.065)	0.058(0.091)	0.102(0.286)	0.046(0.072)
Phosphorus — inorganic PO_4	0.019(0.013)	0.011(0.022)	0.099(0.010)	—
— total	0.162(0.692)	0.012(0.015)	0.006(0.005)	0.012(0.007)
Silica — reactive SiO_2	5.5(1.3)	5.6(1.7)	2.3(0.5)	2.5(0.6)
Number of samples[a]	73	132	171	27
Years collected	1965 to 1977	1965 to 1977	1966 to 1980	1967 to 1978

[a] Samples sizes vary somewhat depending on analyses.

Bay and estuary. Landings between 1951 and 1971 fluctuated between 64 and 394 metric tons (t) and averaged about 168 t (Fig. 5). Because of low stock levels, commercial fisheries were closed from 1972 to 1980 and from 1983 to present; catches during those years (Fig. 5) were incidental catches in non-salmon gear. More than 50 % of large multi-sea-winter (MSW) salmon from the Miramichi are also caught in interceptory fisheries off west Greenland and Newfoundland during their feeding migrations at sea (Pippy 1982). However, it is not possible to identify Miramichi salmon in these fisheries and their landings from these areas are not available.

In Miramichi River proper, anglers exploit anadromous salmon during both their upstream migration when they are called bright salmon (June to October) and during their post-spawning migration to sea as kelts in early spring (April to May). To Show annual fluctuations in angling catches, kelts (year *i*) were added to bright salmon catches in the previous year (year *i*-1). Annual landings have averaged 70 t since 1950 (Fig. 6). Effort (rod-days) steadily increased between 1971 to 1983 from about 48 000 to 94 000 rod-days. CPUE in recent years, however, declined from 1.4 (1972) to 0.3 (1983) kg•rod-day^{-1}.

Currently, the salmon fishery is managed on the basis of satisfying a minimum spawning requirement of 23 600 MSW salmon and 22 600 1-sea-winter (1SW) salmon (Randall 1985). Because of the large size of the Miramichi River, current escapement levels are estimated by indirect methods, including counts at an index trap at Millbank, parr densities from electrofishing surveys and angling exploitation rates (Randall and Chadwick 1983). Returns of MSW salmon are predicted from returns of 1SW salmon in the current year (Marshall et al. 1982). Recent assessments indicated spawning requirements were not being met (Randall and Chadwick 1983; Randall et al. 1985) and current production of salmon in the Miramichi is less than potential production (Table 4).

Gaspereau accounts for the largest biomass of fish of all commercial fisheries in the Miramichi River (Fig. 5). The gaspereau fishery includes two species, alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*); the relative contribution of each species varies considerably from one year to the next (Alexander and Vromans 1985). Catch statistics since 1950 show large annual fluctuations with a maximum catch (both species) in 1952 of 11 600 t followed by a severe decline to 119 t in 1964. Annual landings for the 35-yr period averaged 2 128 t. Licensed trap nets decreased from a maximum of over 200 in the early 1950's to about 35 since 1975 (Alexander and Vromans 1983).

Despite decreased fishing effort in recent years, fishing pressure on gaspereau stocks still appears to be excessive.

TABLE 3. List of freshwater and diadromous fishes inhabiting the Miramichi and Exploits rivers. X indicates species are present and H indicates they are present and harvested.

	Miramichi	Exploits
Diadromous		
Atlantic salmon (*Salmo salar*)	H	H
Alewife (*Alosa pseudoharengus*)	H	
Blueback herring (*Alosa aestivalis*)	H	
American shad (*Alosa sapidissima*)	H	
Brook trout (*Salvelinus fontinalis*)	H	H
Rainbow smelt (*Osmerus mordax*)	H	
Striped bass (*Morone saxatilis*)	H	
Atlantic tomcod (*Microgadus tomcod*)	H	
Sea lamprey (*Petromyzon marinus*)	X	
Atlantic sturgeon (*Acipenser oxyrhynchus*)	X	
American eel (*Anguilla rostrata*)	H	X
Freshwater		
Brook trout (*Salvelinus fontinalis*)	H	H
Atlantic salmon (*Salmo salar*)	H	H
Arctic char (*Salvelinus alpinus*)		H
White sucker (*Catostomus commersoni*)	X	
Golden shiner (*Notemigonus crysoleucas*)	X	
Common shiner (*Notropis cornutus*)	X	
Creek chub (*Semotilus atromaculatus*)	X	
Fallfish (*Semotilus corporalis*)	X	
Pearl dace (*Semotilus margarita*)	X	
Redbelly dace (*Chrosomus eos*)	X	
Finescale dace (*Chrosomus neogaeus*)	X	
Lake chub (*Couesius plumbeus*)	X	
Blacknose dace (*Rhinichthys atratulus*)	X	
Brown bullhead (*Ictalurus nebulosus*)	X	
Banded killifish (*Fundulus diaphanus*)	X	
Mummichog (*Fundulus heteroclitus*)	X	
Nine-spine stickleback (*Pungitius pungitius*)	X	
Three-spine stickleback (*Gasterosteus aculeatus*)	X	X
Brook stickleback (*Culaea inconstans*)	X	
White perch (*Morone americana*)	X	
Yellow perch (*Perca flavescens*)	H	
Slimy sculpin (*Cottus cognatus*)	X	

Biological assessments have been carried out annually since 1982 for each species separately, using commercial catch and effort data and biological information from the Millbank trap (Alexander and Vromans 1983, 1985). These assessments indicte a high rate of exploitation, averaging about 63 % from 1981 to 1984. Recent catches have been based primarily on young fish: for example, the 1984 catch comprised 92 % age 5 or less compared to only 28 % in 1980 when landings were much higher (Fig. 5).

A commercial fishery for rainbow smelt in the Miramichi estuary occurs in winter (December to February) using box nets set under the ice. Total landings from 1950 to 1984 averaged about 400 t annually (Fig. 5). The fishery is based mainly on two age-groups (ages 2 and 3 comprise 94 % of landings; McKenzie 1964). Some smelt are also caught by recreational fishermen during their spawning runs into rivers, but these landings are incidental compared to commercial catches (Table 5). Tagging studies conducted in 1946–47 indicated a total population of about 375×10^6 fish, while landings in that year were about 13.7×10^6 smelt (assuming 26.5 smelt per kilogram; McKenzie 1964) or about 4 % of the total population.

TABLE 4. Estimates of potential production of Atlantic salmon in the Miramichi River and accessible areas of Exploits River, and actual production, 1980 to 1985.

	Miramichi	Exploits
Rearing area (m^2)	55×10^6	9.6×10^6
Potential smolt production		
No.$\cdot$m^{-2}	0.05	0.03
Total	2.75×10^6	288 000
Potential adult production		
1SW	226 875	47 520
2SW	201 099	
Estimated adult production		
Returns to river, 80'–85'		
1SW	51 800	14 200
MSW	26 200	
Total production, 80'–85'		
1SW	57 556	31 600
MSW	43 667	
Percent of potential production		
1SW	25 %	67 %
MSW	22 %	

Data sources: References for rearing area and potential smolt production in text. Miramichi River: potential adult production assumes a 1 : 1 ratio of 1SW to 2SW salmon, 16.5 % of smolts will survive to the 1SW stage (Chadwick et al. 1985a), and mortality in the second year at sea is 1 % per month (Doubleday et al. 1979), returns to river from Randall and Schofield (1987), total production assumes 10 % of 1SW and 40 % of MSW salmon were harvested in high-seas fisheries (Table 12). Exploits River: potential adult production assumes 16.5 % of smolts will survive to become 1SW, returns to river from Table 8, and total production assumes a 55 % exploitation rate at sea (Pippy 1982).

Atlantic tomcod in the Miramichi River spawn in December and January, and are present in the estuary from September until June. Most of the commercial catch occurs in January and February; annual landings averaged 106 t from 1967 to 1984 (range 17–206 t; Fig. 5). Most tomcod are caught incidently in gear licensed for smelt.

Both American shad and striped bass are caught incidently in commercial gear (gill nets and trap nets) set in the Miramichi estuary for Atlantic salmon and gaspereau. Before 1972, there was a gill net fishery for shad in outer Miramichi Bay, but this fishery was discontinued when commercial salmon fishing was banned in 1972. Average catches, 1967 to 1984, were 10 t of shad and 4 t of bass. Both species are caught by anglers and there has been a dramatic increase in their popularity in recent years, particularly for striped bass (Table 5).

Brook trout is the most sought after species by anglers in the Province. Sales of non-salmon angling licenses, which are mainly for trout, have tripled over the last 15 years from about 50 000 in 1970 to over 160 000 in 1985 (M. Redmond, Department of Natural Resources and Energy, Fredericton, New Brunswick, pers. comm.). In Miramichi River, angling effort for species other than salmon (mainly trout) exceeded salmon angling effort by 3 times in 1980. Catches of trout were estimated to be 109 and 59 mt in 1975 and 1980, respectively, exceeding 500 000 fish in both

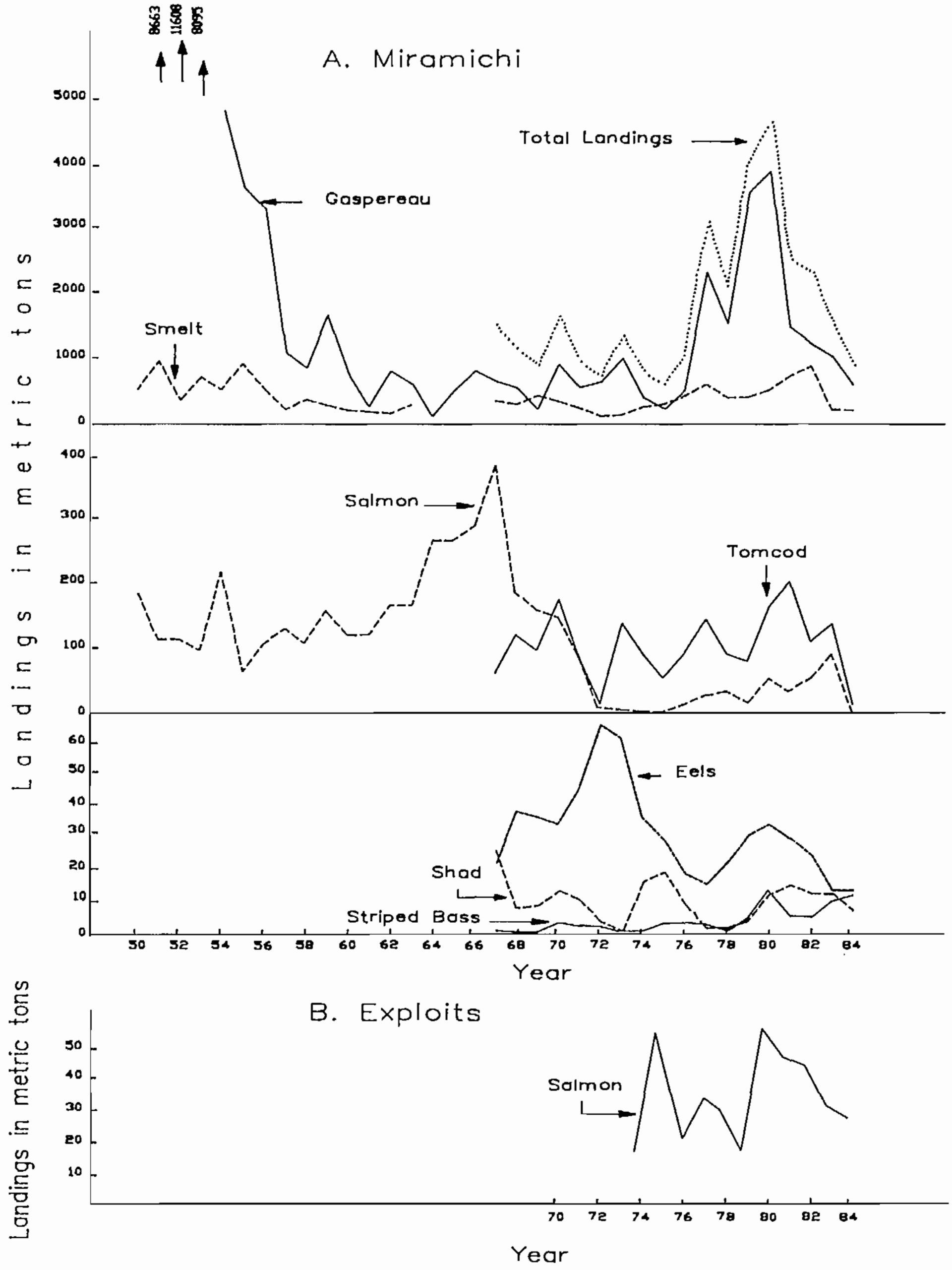

FIG 5. Annual landings (metric tons) of fish from commercial fisheries in Miramichi River (A) and Exploits River (B). Data from Alexander and Vromans (1983; 1985) May and Lear (1971), McKenzie (1964), and unpublished sources.

years (Table 5). These landings also include anadromous trout, but their relative contribution to catches is not known. With the exception of a daily bag limit (15 fish) and regulated fishing seasons, there are few restrictions on the harvest of this species.

From 1967 to 1984, an average of 32 t of eels were landed by commercial fishermen in Miramichi Bay (Fig. 5). Very little is known about the distribution or biology of this catadromous species in the Miramichi River. Aside from a minimum size limit of 8 cm, there are few restrictions on the fishery for eels; effort and catches are determined by market demand. Philpott (1978) provides a map showing the distribution of eel traps in Miramichi Bay.

3.2 Exploits River

Atlantic salmon from Exploits River are caught in a mixed-stock commercial gill net fishery in Bay of Exploits. Total landings of salmon (1SW and MSW salmon) from Bay of Exploits from 1974 to 1984 are illulstrated in Fig. 5. There is a significant correlation between catches of 1SW salmon in Bay of Exploits and total river escapement (angling catch plus counts at Bishops Falls) (Fig. 7). Commercial catches of 1SW salmon from 1980 to 1984 were higher than in previous years (1974 to 1979, with the exception ot 1975), but the difference between periods was not significant (Mann-Whitney test, P = 0.10). Increased

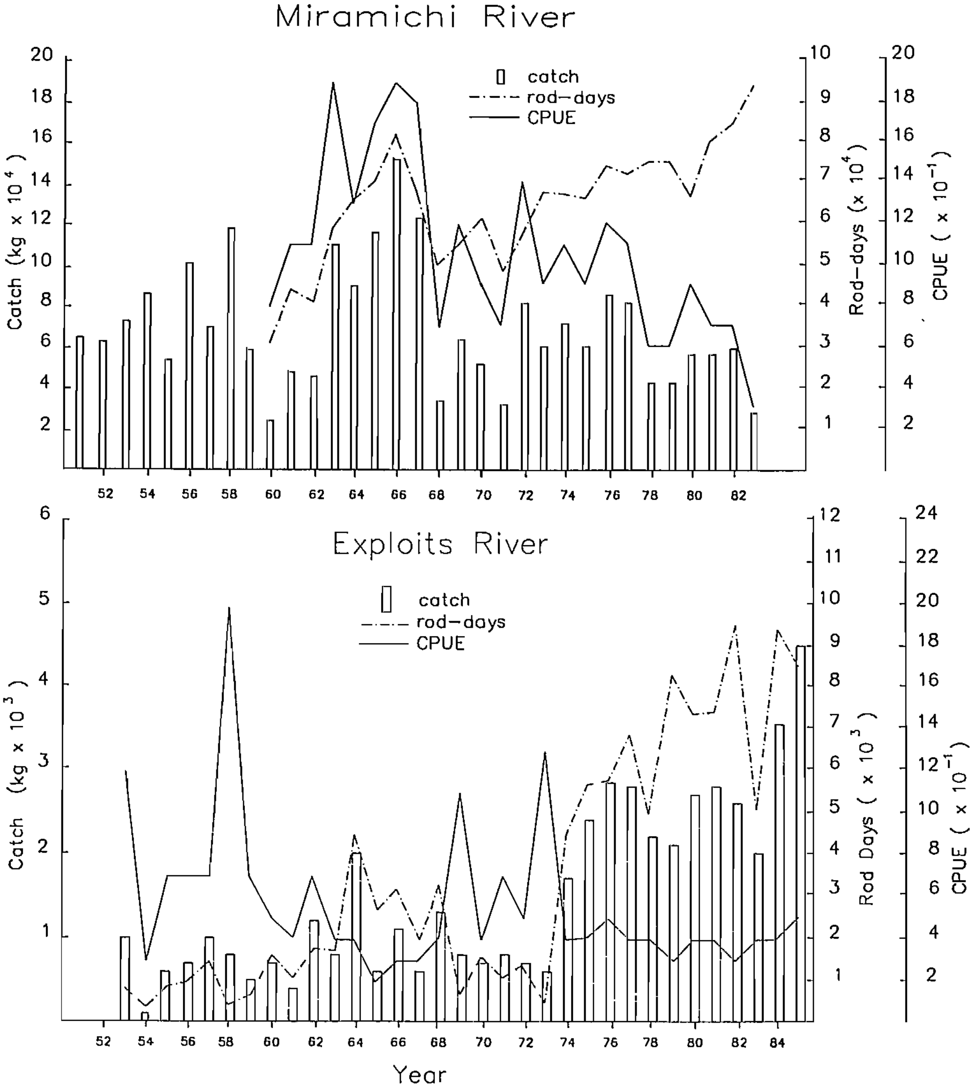

FIG 6. Annual angling statistics for Atlantic salmon in Miramichi River (upper) and Exploits River (lower), 1951 to 1985. Miramichi data from Smith (1981), Swetnam and O'Neil (1985), Hooper (1974, 1978) and New Brunswick Department of Natural Resources and Energy, unpublished sources. Exploits data from O'Connell (unpublished).

catches of 1SW salmon since 1980 have most likely resulted from enhancement activities. Annual commercial landings since 1974 have averaged 35 t, but the proportion of Exploits salmon in these landings is not known.

Most salmon angling on the Exploits River occurs below the dam at Bishop's Falls (Fig. 3). Landings show two distinct periods in angling success: both catches and effort (rod-days) from 1975 to 1985 were greater (Mann-Whitney test, $P < 0.001$) than for the period 1957 to 1974 (Fig. 6). Increased catches in recent years are most likely the result of enhancement programs in the Exploits River. Average angling catches, 1975 to 1985, were 2.8 t annually and CPUE averaged 0.4 kg•rod-day^{-1}.

Unlike the Miramichi River, an assessment of the Exploits River salmon is not prepared each year. However, data from the Exploits, including counts of salmon at fishways, and recreational and commercial catch and effort statistics are incorporated into an overall assessment of Newfoundland salmon stocks each year (e.g. O'Connell et al. 1985). A combination of natural spawning and fry stocking activities have probably maintained Exploits salmon at levels close to carrying capacity (O'Connell et al. 1983) in recent years (Table 4).

In addition to anadromous Atlantic salmon, anglers harvest landlocked salmon, brook trout (including anadromous trout) and arctic char throughout the Exploits watershed. Unfortunately, there are no records of catches for these other species. In recent years, there have been unsuccessful attempts to establish a commercial eel fishery.

4. Fish Production and Yield

4.1 Methods

Fish production was estimated roughly for fluvial habitat of freshwaters of both rivers. Production is defined as total

TABLE 5. Estimated catches[a] of fish by recreational fishermen in the Miramichi River, 1975 and 1980. Data sources: salmon catches from Fig. 6; catches of other species from Hooper (1979, 1982). License data from M. Redmond, New Brunswick Department of Natural Resources and Energy, Fredericton, personal communication.

	1975		1980	
	Number	Kilograms	Number	Kilograms
Atlantic salmon				
anadromous	26 757	64 850	22 289	55 468
landlocked	50	35	—	—
Brook trout	545 272	109 054	656 418	59 078
Yellow perch	9 998	1 000	3 437	309
American smelt	81 494	1 630	71 041	1 421
American shad	120	132	950	1 083
Striped bass	50	35	4 557	3 099
Effort (angler days)	267 112		276 747	
Licenses (New Brunswick)				
Salmon	16 828		20 633	
Non-salmon	110 039		139 568	
Total	126 867		160 201	

[a] For species other than anadromous salmon, angling catches include fish that were subsequently released by anglers. Kilograms were estimated using average weights of each species for the entire province (Hooper 1979, 1982) times the Miramichi catch in numbers.

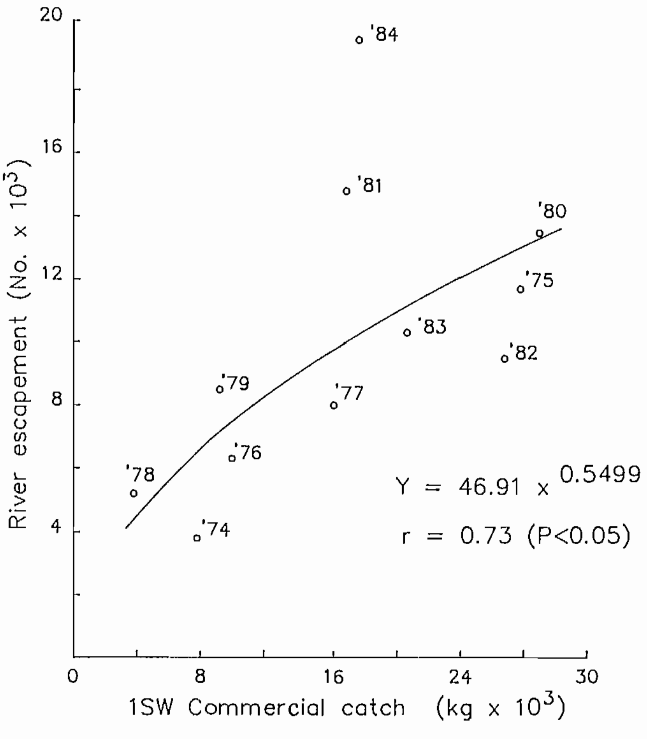

FIG 7. Correlation between commercial catch of 1SW salmon in Bay of Exploits and total salmon escapement into the Exploits River (angling catch plus counts at Bishops Falls).

elaboration of fish tissue per year ($g \cdot m^{-2} \cdot yr^{-1}$), including production by individuals that do not survive to the end of the year (Ivlev 1966). Production in the Miramichi River was calculated by two methods: (1) from estimates of growth and biomass of fish using data from electrofishing surveys and (2) production of juvenile salmon was also calculated from smolt migrations using back-calculated estimates of numbers and biomass.

Electrofishing surveys have been used to measure fish densities in the Miramichi River since 1970. Sites were originally selected in areas of typical salmon habitat (Peppar and Schofield 1978): flowing water averaging 10 to 50 cm in depth with varying proportions of cobble/boudler substrate. Less than 10% of the area of survey sites was pool habitat. Sites averaged 300 m^2 in area (range 144–870) and were located on main trunk and headwater tributaries (stream orders 2 to 6). Sites were enclosed with barrier nets (0.3 cm mesh) and densities were estimated using catch-depletion data (Zippin 1956) from a series of 4 to 6 electrofishing sweeps. All salmon were measured (fork length, nearest 0.5 cm). Other species were not measured, but average weights of sculpins, trout and dace were obtained at 4 sites in 1977–78 (Randall 1981). Data from 27 sites surveyed annually from 1972 to 1983 were used to estimate salmon production (Randall and Chadwick 1986). Production was calculated using an exponential model for growth and assuming a linear change in biomass (Chapman 1978; Ricker 1975). Production of sculpins, trout and dace was estimated from biomass data from the 27 sites, assuming a P/B ratio of 1.2 for all species. A ratio of 1.2 was calculated for Atlantic salmon in the Miramichi River, and Welcomme (1985) found an average P/B ratio of 1.2 (± 0.5) for 95 observations on river populations of fish he summarized.

There have been no quantitative electrofishing surveys in Exploits River. However, it is known from fishway counts and other surveys that salmon are the most abundant migratory species. Production of salmon was back-calculated from estimated carrying capacity of habitat to produce smolts. Specifically, annual salmon production was roughly estimated from smolt data from both rivers using the formula:

$P = GB_0 \, (e^{G-Z}-1)/G-Z$ (Ricker 1975)

G = instantaneous growth = $\ln W_2 - \ln W_1$; where W_2 (mean weight of smolts) was 25 g for Miramichi River (Randall, unpublished data) and 54 g for Exploits River salmon (O'Connell, unpublished data). W_1 (weight of emergent fry) was assumed to be 0.2 g in both watersheds (Randall 1982; Porter and Meerburg 1977).

Z = instantaneous mortality = $-(\ln N_2 - \ln N_1)$; where N_2 was the number of smolts (m^{-2}) and N_1 was numbers of emergent fry. N_1 was calculated assuming an egg to smolt survival rate ranging between 0.01 and 0.05 (Symons 1979; Chadwick 1982) and an egg to emergent fry survival of 0.50. There are few good estimates of egg to emergent fry survival rates in the literature; estimates vary from <0.30 (Peterson 1978; Sturge 1968) to >0.80 (Shearer 1961; Elliott 1984). For estimating production from the above formula, we assume that year-class production was equal to annual production.

B_0 = initial biomass = $W_1 \cdot N_1$

There have been no quantitative estimates of fish biomass and production in lacustrine habitat of the Exploits River. However, an indication of fish productivity in lakes was inferred from studies in other Newfoundland rivers.

Total fisheries yield ($kg \cdot ha^{-1} \cdot yr^{-1}$), including biomass produced in the marine environment by anadromous species, was summarized for both rivers.

4.2 Results

4.2.1 Fluvial production

In Miramichi River, four species made up most of the fish community in fluvial habitat surveyed by electrofishing: Atlantic salmon were most abundant (average 0.37 fish•m^{-2}), followed by blacknose dace (0.13 fish•m^{-2}), slimy sculpins (0.13 fish•m^{-2}) and brook trout (0.02 fish•m^{-2}) (Fig. 8). Other species (Table 3) averaged 0.05 fish•m^{-2}, making a total fish density of about 0.70 fish•m^{-2}.

Juvenile Atlantic salmon normally smoltify after 3 years in the Miramichi River (Randall, personal observation) and thus 3 age-groups made up the juvenile populations, age 0+ fry and ages 1+ and 2+ parr. Biomass and production of salmon were low: biomass averaged 1.03 g•m^{-2} (annual means ranged from 0.52 to 1.32 g•100 m^{-2}) (Table 6) while production averaged 1.26 g•m^{-2}•yr^{-1} (0.68 to 1.61 g•m^{-2}•yr^{-1}) (Randall and Chadwick 1986). The ratio of production to average biomass (P/B ratio), which is an estimate of annual growth rate (instantaneous) or turnover rate, averaged about 1.2 for all year-classes combined.

Juvenile salmon densities were probably below carrying capacity of the environment in most years (Randall and Chadwick 1986). Under optimum spawning conditions, salmon habitat in the Miramichi River can produce 0.05 smolts per m^2 on average (Elson 1975). This estimate appears reasonable or even conservative because total smolt output from 1954 to 1971 averaged 0.039 smolts•m^{-2} (SD = 0.028, range = 0.01–0.10; calculated from data in Paloheimo and Elson [1974]). Total freshwater production of salmon required to produce 0.05 smolts was estimated to be between 2 and 4 g•m^{-2}•yr^{-1} (Table 7).

TABLE 6. Estimated freshwater biomass (g•m^{-2}) of salmon, trout, dace, and sculpins in the Miramichi River, 1972 to 1983. Values are averages for 27 sites monitored each year (see text).

Year	Salmon	Trout	Dace	Sculpin	Total
1972	0.92	0.38	0.60	0.35	2.25
1973	0.52	0.16	0.29	0.54	1.51
1974	1.19	0.20	0.38	0.42	2.19
1975	1.32	0.21	0.47	0.41	2.41
1976	1.24	0.14	0.54	0.44	2.36
1977	1.29	0.18	0.30	0.46	2.23
1978	1.04	0.13	0.32	0.57	2.06
1979	0.88	0.04	0.26	0.59	1.77
1980	0.89	0.05	0.29	0.47	1.70
1981	1.00	0.04	0.26	0.35	1.65
1982	1.01	0.07	0.36	0.43	1.87
1983	1.04	0.10	0.31	0.31	1.76

Applying average weights of dace, sculpins and trout from 4 sites surveyed in 1977 and 1978 gave a total average biomass of roughly 0.95 g•m^{-2} (Table 6). Total biomass of the four dominant species was, therefore, 1.98 g•m^{-2} of which salmon contributed 50 %. Assuming the P/B ratio calculated for salmon applies to these other species as well, the above biomass indicates a production rate of about 2 g•m^{-2}•yr^{-1}. If salmon populations were at carrying capacity, total production based on these rough calculations and assuming the biomass of other species remains at present levels, could range between 3 and 5 g•m^{-2}•yr^{-1} in fluvial habitat of the Miramichi River.

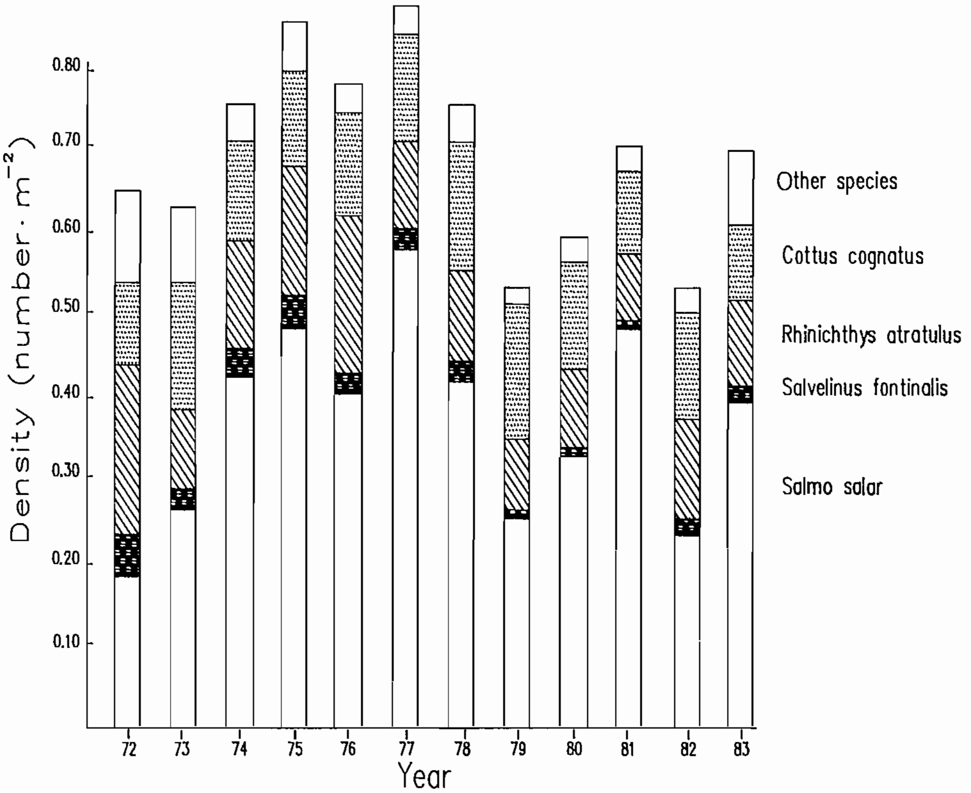

FIG 8. Average densities of fish (number•m^{-2}) at 27 electrofishing sites in Miramichi River (1972 to 1983).

Production of salmon in riverine habitat of the Exploits River was calculated from estimated yields of smolts. Atlantic salmon in the Exploits smoltify at ages 3 and 4 (O'Connell et al. 1983). Total smolt output was estimated for Great Ratting Brook and the middle Exploits by back-calculating from the known adult returns (Table 8), assuming a return rate of 6% from smolts to 1SW salmon (Chadwick and Meerburg 1978). In both areas, smolt yield averaged about 0.03 smolts•m^{-2} (Table 9), and this is considered optimum for most rivers in insular Newfoundland (O'Connell, unpublished data). Freshwater production required to yield these smolts was estimated to be 3 to 4 g•m^{-2}•yr^{-1} (Table 7). Although fewer smolts per unit area are produced in the Exploits than in the Miramichi River, production rate is similar because Exploits smolts are larger (54 g versus 25 g) and older (mean age of 3.4 versus 2.7 yr). Brook trout and American eels are the only other species common in fluvial habitat of the Exploits. In the absence of quantitative data on their abundance and assuming they are less abundant than salmon as in the Miramichi, production may be increased by 10–30% to account for them, making a total fluvial production rate of 3–5 g•m^{-2}•yr^{-1} in the Exploits River.

4.2.2 Lacustrine Production

Although no studies have been made of fish production in lakes within the Exploits River, studies in other Newfoundland rivers provide data that may be applicable to the Exploits. Ryan (1984, 1986, and personal communication) monitored salmon and trout populations in two small, shallow lakes of the Gander River which is adjacent to the Exploits. From 1979 to 1983, biomass averaged 0.10 g•m^{-2} for salmon and 0.29 g•m^{-2} for trout. Chadwick and Green (1984) estimated salmon production to be low in lakes of Western Arm Brook in western Newfoundland; production was estimated at 0.07 g•m^{-2}, but because lacustrine habitat represented 98.5% of the rearing habitat in this watershed, 67% of smolts were produced in standing waters. Although previous estimates of potential Atlantic salmon production in Newfoundland rivers have considered only fluvial habitat (e.g. Pippy 1982), it is clear that production within lakes is also important.

TABLE 7. Production of salmon (g•m^{-2}•yr^{-1}) required to yield 0.03 smolts (Exploits) or 0.05 smolts (Miramichi) per m^2, assuming survival from eggs to smolts ranging between 0.01 and 0.05, and survival from egg deposition to alevin emergence of 0.50. Details of methodology in text.

Survival egg to smolts	Smolt yield•m^{-2}	
	0.03	0.05
0.01	4.4	4.0
0.03	3.1	2.7
0.05	2.7	2.2

TABLE 9. Estimated numbers of smolts produced in the Miramichi and Exploits rivers.

		Exploits	
	Miramichi	G. Rattling Bk	Middle Exploits
Rearing area	55 × 10^6	32 488	18 280
Study period	1951–71	1980–85	1980–85
Smolts			
mean (no.•m^{-2})	0.04	0.03	0.03
range	(0.01–0.10)	(0.02–0.04)	0.02–0.05)

In the previous section, all salmon smolts in the Exploits River were assumed to come from fluvial habitat. If significant salmon production occurs in lacustrine habitat, then we significantly overestimated production rates in fluvial habitat. This uncertainty would not affect the Miramichi, where lacustrine habitat is rare.

4.2.3 Fisheries Yield

Fisheries yield in both the Miramichi and Exploits rivers is only indirectly related to freshwater production. Most commercial and angling fisheries are based on anadromous fishes (Table 3), and most growth and production of these species occurs in estuarine and marine environments. Depending on species, from 60 to 100% of total growth in length occurs at sea (Table 10). Even for Atlantic salmon, which reside in freshwater for a relatively large proportion of their life cycle (2–6 yr), most growth (>70%) occurs in the marine environment. For these species, fisheries yield is not restricted by the apparently unproductive freshwater environment of these rivers.

Total yield from each river is given in Table 11. Average fisheries yield was 550 kg•ha^{-1}•yr^{-1} in Miramichi River and 40 kg•ha^{-1}•yr^{-1} in Exploits River.

5. Factors Affecting Production and Yield of Fisheries

Three man-related factors have affected production of fish in the Miramichi and Exploits rivers: fishing exploitation,

TABLE 8. Returns of adult Atlantic salmon to Great Rattling Brook and the middle Exploits, and estimated smolt outputs the year before.

Year (*i*)	Angling catch (no.) below Bishop's Falls (year *i*)	Bishop's Fall adult count (year *i*)	Total river escapement (no.) (year *i*)	Great Rattling Brook adult count (year *i*)	Middle Exploits adult count (year *i*)	Total smolt output (no.) (year *i*-1)	Great Rattling Brook smolts (no.) (year *i*-1)	Middle Exploits smolts (no.) (year *i*-1)
1980	1 417	12 002[a]	13 419	4 968	3 073	223 650	92 576	57 264
1981	1 556	13 167[a]	14 723	4 800	4 022	245 383	89 454	74 955
1982	1 519	7 981[a]	9 500	2 959	2 388	158 333	58 703	47 375
1983	527	9 663[a]	10 190	4 254[a]	2 220	169 833	74 767	39 018
1984	1 809	17 744	19 553	6 609[a]	5 074	325 883	121 380	93 188
1985	903	16 829	17 732	6 025	5 003	295 533	105 805	—

[a] Estimated.

TABLE 10. Approximate length of freshwater residence and relative growth in freshwater and marine environments of anadromous fish inhabiting the Miramichi and Exploits rivers.

Species	Freshwater residence	Approximate size (mm) hatching	smolting	maturity	% growth in freshwater
Alewifes	3-5 mo	5	55–109	250-300	17–42 %
Blueback herring	3-5 mo	5	30–50	250–300	8–18 %
Shad	2–3 mo	15	37–112	460	2–18 %
Salmon					
Miramichi	2–4 yr	25	150	730	18 %
Exploits	2–6 yr	25	175	520	30 %
Striped bass	(incubation)	—	—	—	0%
Smelt	2–4 wk (incubation)	5	5	140	0 %

TABLE 11. Summary of recorded harvest of fish in the Miramichi and Exploits rivers. Relative harvest (kg•ha^{-1}) is based on 5 500 ha and 508 ha of rearing area in the Miramichi and Exploits rivers, respectively.

	Years in mean	Mean annual harvest kg	kg•ha^{-1}
	Miramichi River		
Angling			
Salmon	1950–1983	70 200	12.8
Trout	1975, 1980	84 100	15.3
Others	1975, 1980	4 400	0.8
Total		158 700	28.9
Commercial			
Gaspereau	1950–1984	2 127 000	386.7
Smelt	1967–1984	418 000	76.0
Salmon	1950–1971	168 000	30.5
Tomcod	1967–1985	106 000	19.3
Eels	1967–1984	32 000	5.8
Shad	1967–1984	10 000	1.8
Bass	1967–1984	4 000	0.7
Total		2 865 000	520.8
	Exploits River		
Angling			
Salmon	1975–1985	2 800	5.5
Trout		Unknown	
Others		Unknown	
Total		2 800	5.5
Commercial			
Salmon	1974–1984	16 900	33.3
Total		16 900	33.3

habitat perturbations and enhancement programs. Although all three factors have undoubtedly affected many fish species, their impact on Atlantic salmon populations has been documented in the most detail.

5.1 Fishing Exploitation

Using early catch statistics (1870–1930), Huntsman (1931) was the first to investigate whether or not commercial fisheries were having an adverse effect on Atlantic salmon spawning levels in the Miramichi River. Although noting large fluctuations in landings among years, Huntsman found no evidence that stocks were being overfished even after the onset of the large drift net fishery in Miramichi Bay during the early 1900's.

More recent research, however, has indicated otherwise. Smolt tagging studies in the 1950's and 1960's showed fishing exploitation was excessive with commercial fisheries accounting for over 80 % of recaptures of large salmon (Table 12; Saunders 1969; Kerswill 1971). With the onset of the international fishery for salmon off Greenland, where significant numbers of Miramichi large salmon are intercepted, overfishing became critical. Paloheimo and Elson (1974) documented in detail the impact of the Greenland fishery and noted a significant negative correlation between percentage returns in the Miramichi River and catches in Greenland the year before. Decreased returns to the river, as indicated in counts on the Northwest Miramichi counting fence and at Millbank (Fig. 9), prompted a total ban on homewater commercial fisheries from 1972 to 1980. Unfor-

TABLE 12. Percent recaptures of Miramichi tagged smolts at homewater and high-seas fisheries. Northwest Miramichi data from Paloheimo and Elson (1974). Entire Miramichi data from J. Ritter (Department of Fisheries and Oceans, Halifax; unpublished data).

	1SW salmon Escapement	Angling	Commercial Home	High-seas	MSW salmon Escapement	Angling	Commercial Home	High-seas
Northwest								
1950–61	46	20	16	18	18	4	58	20
1960–63	63	20	14	4	3	15	52	30
1964–65	44	33	17	6	3	6	57	34
1966–68	32	36	25	7	4	8	51	37
Miramichi								
1968–74	62	21	3	14	22	7	8	63
1982–83				10				40

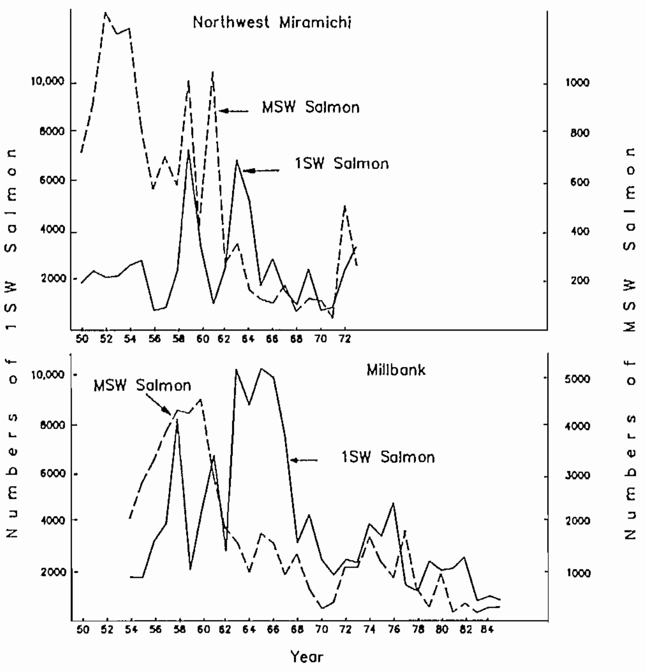

FIG 9. Counts of 1SW and MSW salmon at the Northwest Miramichi counting fence, 1950 to 1973, and Millbank trap, 1954 to 1985.

tunately, catches of salmon in non-salmon gear increased during this period and, in some years, was significant (e.g. 68 t in 1980; Fig. 5). Commercial fisheries reopened from 1981 to 1983, but were controlled by quota. Continued poor returns prompted another commercial closure in 1984 and this closure has continued to date.

Anglers also have a significant impact on Miramichi salmon. Randall and Chadwick (1983) estimated anglers remove about 25 % of all salmon that enter the river. Elson (1974) provides evidence that angling exploitation rate may increase up to 80 % in some years, especially when salmon returns are low.

Several facts indicate freshwater production and yield of salmon in the Miramichi is controlled by spawning escapement, which in turn is controlled by fisheries. Fry densities (as measured by electrofishing surveys) were significantly and positively correlated with salmon spawners the year before as counted at a fence in the Northwest Miramichi from 1951 to 1971 (Paloheimo and Elson 1974). A similar correlation was found between parr and spawners in the entire Miramichi in more recent years (1969–82) (Chadwick and Randall 1986). In the latter correlation, angled kelts were used as an index of spawners. The fact that a linear regression best described the relationship between spawners and their progeny suggested that spawning levels were below optimum. In rivers where spawning is adequate, parr densities either remain constant or may even be reduced at high spawning levels (Solomon 1985). A detailed analysis of growth, biomass and production of juvenile salmon in the Miramichi River indicated production was generally linearly correlated with initial fry densities, verifying that parr densities were below carrying capacity (Randall and Chadwick 1986). Similar influences of spawning stock on production and yield of salmon in other Canadian rivers have been discussed by Chadwick (1985).

Estimates of commercial fishing exploitation rate on Exploits River salmon have not been made, but it is probably not excessive. Exploits salmon mature mainly as 1SW fish (large salmon are repeat spawners) which are not intercepted in the Greenland fishery (Ruggles and Ritter 1980). Pippy (1982) estimated about 55 % of Newfoundland salmon are taken in local commercial fisheries and this rate may apply to the Bay of Exploits commercial fishery. Angling exploitation rate averaged about 14 % between 1980 and 1985.

5.2 Habitat Perturbations

Habitat perturbations and their effects on fish popultions have been well documented in the literature for both the Miramichi (Elson 1967, 1974; Elson et al. 1972; Logie 1975 and Philpott 1978) and Exploits rivers (Taylor and Bauld 1973; Wilson 1974; Farwell 1975; and Morry and Cole 1977). Therefore, only a brief synopsis will be given here.

Forest spraying to control spruce budworm (*Choristoneura fumiferana*) has caused insecticide contamination in the Miramichi River since 1952. The insecticide DDT was applied to portions of the watershed in cetain years between 1952 and 1964. DDT had both lethal and sublethal effects on juvenile salmon; depending on concentration, up to 90 % of underyearlings and 50 % of parr were killed by DDT directly and sublethal changes in behaviour probably affected their long-term survival as well (Elson 1974). Reductions in adult salmon returns by from 40 to 60 % in the late 1950's and early 1960's, as indicated by angling catches, was probably attributable to the effects of DDT (Elson 1974; Logie 1975). Fenitrothion replaced DDT as the forest insecticide used in New Brunswick in 1963, and its effects on fish are believed to be less damaging. At concentrations used, fenitrothion can have short-term effects on aquatic invertebrate prey of salmon (i.e. increased drift rates), but it does not affect the fish directly (Symons 1977).

Effluents from a base-metal mine established in the headwaters of the Northwest Miramichi caused fall-back and straying of adult salmon from this tributary between 1960 and 1970. Elson et al. (1973) estimated losses to the tributary of 8–15 % of the total run; salmon entering the river late (after 1 August) which normally spawn in the lower reaches were especially affected. Abatement measures, where all effluent was impounded and treated with lime, were implemented in 1971. The mine was closed in 1981.

During the period when insecticides and mining wastes were affecting the upper reaches of the river, industrial pollution in the estuary of the Miramichi was increasing. Pollutants included organic solids in the effluent of pulp and paper mills in Newcastle and Nelson-Miramichi, pentachlorophenol from a wood-preserving plant in Newcastle and untreated sewage from both Newcastle and Chatham (Philpott 1978). Ultrasonic tracking indicated adult salmon moved slowly through polluted portions of the estuary and avoided the Northwest arm because of effluent from the pulp and paper mill in Newcastle (Elson et al. 1972). Elson (1974) presented evidence that these delays in salmon migration caused proportional increases in commercial catches of salmon in outer Miramichi Bay. Many abatement measures to reduce pollution in the estuary were implemented during the 1970's (Philpott 1978).

The Exploits River has also been affected by effluents from pulp and paper and mining operations, but not to the same extent as the Miramichi. A base metal mine began operation at Buchans (Fig. 3) in 1927. Prior to 1966, mine tailings were discharged directly into Buchans Brook where they were carried downstream into Red Indian Lake. Beginning in 1966, however, tailings were treated in a settling pond before being discharged. Morry and Cole (1977) were unable to detect any deleterious effects on Red Indian Lake fish populations from heavy metal concentrations. The mining operation has been phased out in recent years.

A pulp and paper mill was built at Grand Falls in 1909 and effluent from it is discharged directly into Exploits River; however, no quantitative studies have been carried out to identify the impact on fish popultions. Several dams have been constructed on the Exploits in conjunction with pulp and paper operations and to provide hydroelectric power. Locations include: (1) Bishop's Falls; historically this dam was not a complete barrier to anadromous migrations, but fish were delayed during periods of low flow until a fish passage facility was built in 1971; (2) Grand Falls dam, located just upstream from an impassable falls; (3) Goodyears dam and two fishways around it, about 3 km upstream from Grand Falls dam; and (4) Sandy Brook, about 7 km from the mouth, a major tributary of the middle Exploits. Aside from blocking fish passage, these dams have affected fish populations in other ways: Morry and Cole (1977) attributed low fish production in Red Indian Lake to extreme fluctuations in water levels (due to operations of the dam) that created unstable littoral areas. Another major watercourse alteration was the diversion of Victoria River (tributary to Red Indian Lake) to the Bay D'Espoir power project, removing 1 060 km^2 of drainage area from the upper Exploits.

5.3 Enhancement Programs

Historically, < 10 % of the Exploits River was accessible to anadromous salmon due to natural or man-made obstructions listed above. Introductions into areas previously uninhabited by salmon were accomplished by two major enhancement projects: (1) adult salmon transfers into Great Rattling Brook, 1957 to 1965; and (2) stocking fry in tributaries of the middle Exploits (Grand Falls to Red Indian Lake dam, Fig. 3), 1968 to 1980.

Adult salmon were transferred to Great Ratting Brook from an adjacent watershed (Rattling Brook) because hydroelectric development in the donor stream effectively closed this system to salmon. Salmon were released above Camp 1 on Great Ratting Brook (an impassable obstruction) and allowed to spawn naturally; transfers decreased from a maximum of 786 fish in 1958 to 18 fish in 1964, the final year of transfer. A fishway was constructed at Camp 1 in 1960 and counts of adults have increased since, particularly beginning in 1975 (Fig. 10a). Maximum adult escapement (1975) was 6 556 adults. The results of the Great Ratting Brook enhancement project has been well documented (Sturge 1966; Taylor and Bauld 1973; Farwell 1975; O'Connell and Bourgeois 1987).

Broodstock for stocking above Grand Falls came from a tributary of Humber River, Newfoundland. A spawning channel was built on Noel Paul's Brook (Fig. 3) in 1967 and unfed fry were distributed throughout the tributary beginning in 1968 (Fig. 10b). An adult fishway was completed at Grand Falls in 1974. In 1975, fry production was increased with the use of incubation boxes and broodstock were collected from Great Rattling Brook. Fry stocking was subsequently expanded to include 6 more tributaries of the middle Exploits. Adult returns to Grand Falls fishway increased in 1980, most probably a result of the stockings of fry (Fig. 10b). High returns of adults to Grand Falls have subsequently been maintained. O'Connell et al. (1983), and O'Connell and Bourgeois (1987) have assessed the results of fry stocking in the middle Exploits River.

Counts of salmon at Bishop's Falls, which include fish destined for Great Ratting Brook and the middle Exploits, confirm the increased returns resulting from enhancement activities in recent years (Fig. 10c). These returns have also been reflected in increased returns to commercial and recreational fishermen as was previously described.

Enhancement projects at the Miramichi River have been on a smaller scale than at the Exploits. Most (>95 %) of all habitat is available to migrating salmon, allowing natural spawning to occur. The largest enhancement project has taken place at Bartholomew River (a tributary comprising about 1 % of the total habitat area of the Miramichi) where adult salmon were partially blocked from entering the river by a dam until 1976. Returns of marked adults from hatchery stocking in Bartholomew River have contributed about 31 and 16 % of 1SW and MSW salmon spawners, respectively, since 1972 (Chadwick et al. 1985b).

6. General Discussion

Data on juvenile Atlantic salmon provide the only index for comparing production capacity of fluvial habitat in the Miramichi and Exploits rivers. Our preliminary analyses suggest potential salmon production is similar in the two rivers, ranging between 2 and 4 $g \cdot m^{-2} \cdot yr^{-1}$. Direct comparison between rivers is difficult, however, for three reasons. First, salmon populations in the middle Exploits have been supported by extensive enhancement activities, and whether or not yields of 0.03 $smolts \cdot m^{-2}$ (which the above production estimate is based on) could be maintained with natural spawning requires confirmation. Secondly, estimates of smolt yield in the Exploits were based on the assumption that juvenile salmon inhabit only fluvial habitat; if significant production occurs in lacustrine habitat as well, our estimate of fluvial production is an overestimate. Finally, juvenile salmon in the two rivers are different biologically: Miramichi salmon smoltify at a younger age and are smaller than Exploits salmon. Therefore, although production rates may be similar, final numbers of smolts produced in the Miramichi per unit area are 1.7 times greater than in the Exploits.

Production of all fish species inhabiting fluvial habitat was estimated to range between 3 and 6 $g \cdot m^{-2} \cdot yr^{-1}$ in both rivers. Juvenile salmon were the most abundant species in the Miramichi River, and in the absence of quantitative data on other species, this was also assumed to be the case in the Exploits River when total production was estimated. Production by species other than salmon is almost certainly underestimated in both rivers. Electrofishing sites in the Miramichi River were deliberately selected in prime habitat for salmon; densities of trout and cyprinids would be greater in pool habitat. Also, because electrofishing surveys were conducted only once annually, estimates of seasonal

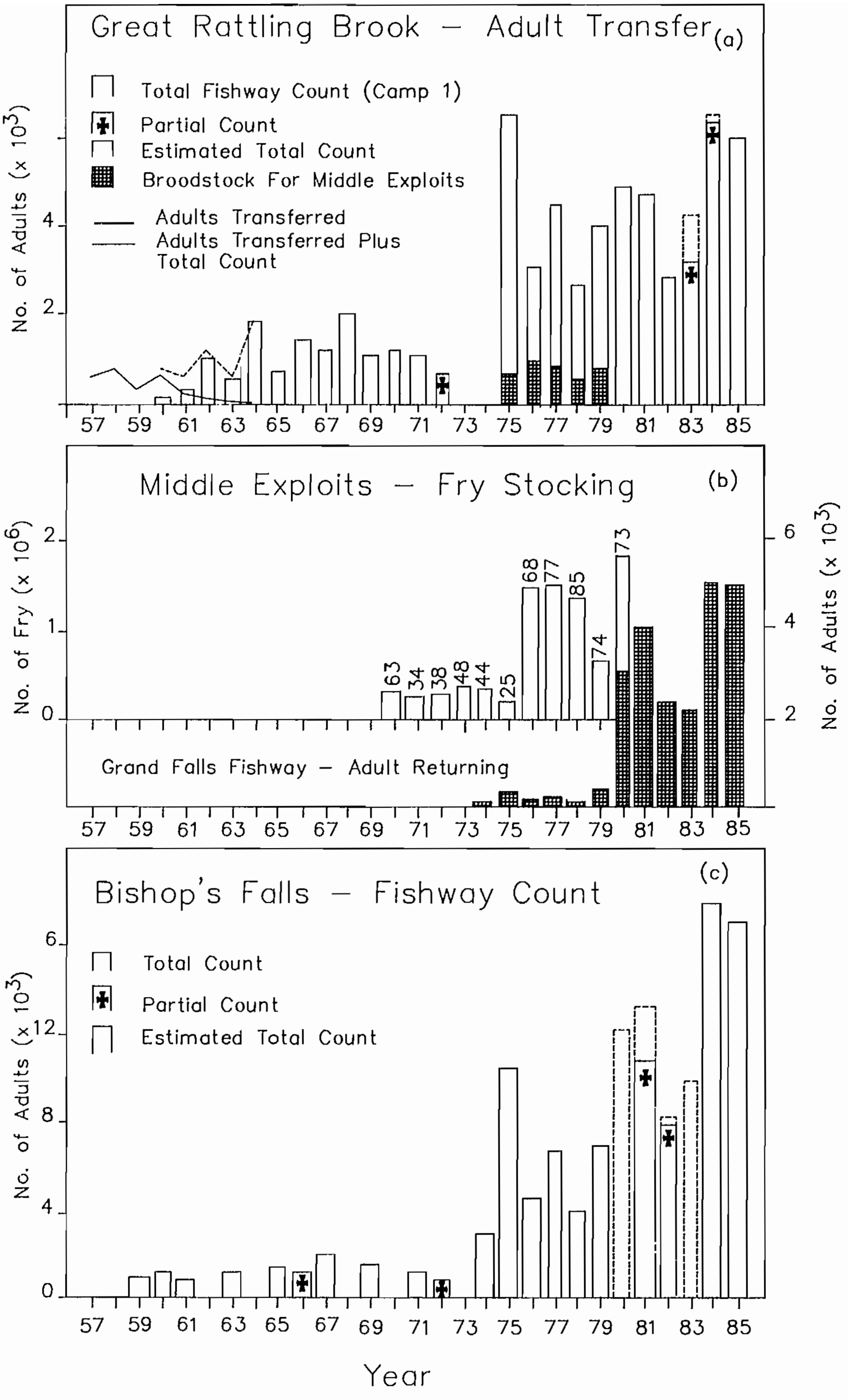

FIG 10. (a) Salmon counts at Camp 1 fishway on Great Rattling Brook and adults transferred into Great Rattling Brook. (b) Numbers and densities (above histogram bars) of fry stocked into the Middle Exploits and adult counts at Grand Falls fishway. (c) Adult counts at Bishop's Falls fishway.

changes in growth and mortality were not available. For all of the above reasons, our estimates of fluvial production are rough approximations only. Nevertheless, our preliminary estimates suggest the productivity of freshwater habitat in both the Miramichi and Exploit rivers is probably low. For several rivers where production has been estimated, Welcomme (1985) noted total community production rates averaged 22 (range 2–200) $g \cdot m^{-2} \cdot yr^{-1}$. The estimate for our two rivers in eastern Canada is near the lower end of this range.

Despite apparently low productivities, total yield to fisheries is quite high in both the Miramichi and Exploits Rivers. This is possible because of the anadromous species inhabiting the rivers for which most growth and production occurs at sea. If all harvests in the Miramichi River, for instance, were dependent on freshwater production, we would not expect landings to exceed 50 $kg \cdot ha^{-1} \cdot yr^{-1}$, assuming (optimistically) that freshwater production is 10 $g \cdot m^{-2} \cdot yr^{-1}$ and 50 % of production is available for harvest. Yet total landings on the Miramichi are 10 times greater exceeding 550 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Table 12). Most of this yield has resulted from marine production, and this emphasizes the importance of anadromous fishes to this river. Recorded landings in the Exploits River are considerably less than in the Miramichi (40 $kg \cdot ha^{-1} \cdot yr^{-1}$; Table 12) in part because recreational harvests of landlocked salmon, arctic char and trout are not recorded, but mainly because of the absence of many of anadromous species found in the Miramichi (Table 3). Nevertheless, fisheries yield capacity in both rivers is greatly enhanced because of the presence of anadromous species. For this reason, estimates of freshwater production rate per se are not a good index of fisheries yield potential in these rivers.

This study has provided some insight into the production and yield of fisheries in the Miramichi and Exploits rivers. More research is required to further refine our estimates of fish production, particularly for species other than Atlantic salmon. It is apparent, however, that management of these rivers must consider proper protection of all freshwater habitat, both for species which reside entirely in freshwater and for anadromous species which depend on freshwater for spawning and nursery habitat. Although apparently unproductive in the classical biological sense, both the Miramichi and Exploits rivers support, directly or indirectly, considerable fisheries resources.

7. References

ALEXANDER, D. R., AND A. H. VROMANS. 1983. Status of the Miramichi River estuary gaspereau fishery (1982). Canadian Atlantic Fisheries Scientific Advisory Committee, Research Document 83/37: 40 p.

1985. Status of the Miramichi River estuary gaspereau fishery (1984). Canadian Atlantic Fisheries Scientific Advisory Committee, Research Document 85/92: 25 p.

AMIRO, P. G. 1983. Aerial photographic measurement of Atlantic salmon habitat of the Miramichi River, New Brunswick. Canadian Atlantic Fisheries Scientific Advisory Committee, Research Document 83/74: 31 p.

ANONYMOUS. 1979. New Brunswick water quality data, 1961–1977. Environment Canada, Inland Waters Directorate, Water Quality Branch, Ottawa. 300 p.

1982. Newfoundland water quality data, 1965–1980. Environment Canada, Inland Waters Directorate, Water Quality Branch, Ottawa. 147 p.

1985. Atlantic provinces historical stream flow summary — to 1984. Environment Canada, Inland Waters Directorate, Water Quality Branch, Ottawa. 236 p.

CHADWICK, E. M. P. 1982. Stock-recruitment relationship for Atlantic salmon (*Salmo salar*) in Newfoundland rivers. Can. J. Fish. Aquat. Sci. 39: 1496–1501.

1985. The influence of spawning stock on production and yield of Atlantic salmon (*Salmo salar* L.) in Canadian rivers. Aquacult. Fish. Manage. 1: 111–119.

CHADWICK, E. M. P., AND J. M. GREEN. 1984. Atlantic salmon (*Salmo salar* L.) production in a largely lacustrine Nefoundland watershed. Verh. Int. Verein. Limnol. 22: 2509–2515.

CHADWICK, E. M. P., AND D. J. MEERBURG. 1978. Sea survival of 1SW Atlantic salmon. Int. Counc. Explor. Sea CM 1978/M: 10: 4 p.

CHADWICK, E. M. P., AND R. G. RANDALL. 1986. A stock-recruitment relationship for Atlantic salmon in the Miramichi River, New Brunswick. North Am. J. Fish. Manage. 6: 200–203.

CHADWICK, E. M. P., D. G. REDDIN, AND R. F. BURFITT. 1985a. Fishing and natural mortality rates for 1SW Atlantic salmon (*Salmo salar* L.). Int. Counc. Explor. Sea CM 1985/M: 18: 11 p.

CHADWICK, E. M. P., D. R. ALEXANDER, R. W. GRAY, T. G. LUTZAC, J. L. PEPPAR, AND R. G. RANDALL. 1985b. 1983 Research on anadromous fishes, Gulf Region. Can. Tech. Rep. Fish. Aquat. Sci. 1420: 69 p.

CHAPMAN, D. G. 1978. Production, p. 202–217. *In* T. Bagenal [ed.] Methods for assessment of fish production in freshwaters. Blackwell Scientific Publications, London.

DOUBLEDAY, W. G., D. R. RIVARD, J. A. RITTER, AND K. U. VICKERS. 1979. Natural mortality rate estimates for North Atlantic salmon in the sea. Int. Counc. Explor. Sea CM 1979/M: 26. 15 p.

ELLIOTT, J. M. 1984. Numerical changes and population regulation in young migratory trout *Salmo trutta* in a Lake District stream, 1966–83. J. Anim. Ecol. 53: 327–350.

ELSON, P. F. 1967. Effects on wild young salmon of spraying DDT over New Brunswick forests. J. Fish. Res. Board Can. 24: 731–767.

1974. Impact of recent economic growth and industrial development on the ecology of Northwest Miramichi Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 31: 521–544.

1975. Atlantic salmon rivers, smolt production and optimal spawning: an overview of natural production. Int. Atl. Salmon Found. Spec. Publ. Ser. 6: 96–119.

ELSON, P. F., A. L. MEISTER, J. W. SAUNDERS, R. L. SAUNDERS, AND V. ZITKO. 1973. Impact of chemical pollution on Atlantic salmon in North America. Int. Atl. Salmon Found. Spec. Publ. 4: 83–110.

ELSON, P. F., L. M. LAUZIER, AND V. ZITKO. 1972. A preliminary study of salmon movements in a polluted estuary, p. 325–330. *In* M. Ruivo [ed.]. Marine pollution and sea life. Fishing News (Books) Ltd., London.

FARWELL, M. 1975. The development of the Exploit's River for Atlantic salmon. Dep. Environ. Fish. Mar. Serv. Int. Rep. Ser. NEW/I-75-3. 49 p.

HOOPER, W. C. 1974. The New Brunswick Atlantic salmon sport fishery, 1969 to 1973. N.B. Dep. Nat. Resourc. Energy, Fish. Manage. Rep. 4: 32 p.

1978. The New Brunswick Atlantic salmon sport fishery, 1962–1977. N.B. Dep. Nat. Resourc. Energy, Fish. Manage. Rep. 7: 49 p.

1979. The 1975 New Brunswick sport fishery. N.B. Dep. Nat. Resourc. Energy, Fish. Manage. Rep. 9, 59 p.

1982. 1980 New Brunswick angler survey. N.B. Dep. Nat. Resourc. Energy. Unpublished report.

HOSIE, R. C. 1969. Native trees of Canada. Canadian Forestry Service, Queens Printer, Ottawa. 380 p.

HUNTSMAN, A. G. 1931. The Maritime salmon of Canada. Biological Board of Canada Bull. XX1: 99 p.

IVLEV, V. S. 1966. The biological productivity of waters. J. Fish. Res. Board Can. 23: 1727–1759.

KERSWILL, C. J. 1971. Relative rates of utilization by commercial and sport fisheries of Atlantic salmon (*Salmo salar*) from the

Miramichi River, New Brunswick. J. Fish. Res. Board Can. 28: 351–363.

Logie, R. R. 1975. Effects of aerial spraying of DDT on salmon populations of the Miramichi River, p. 293–300. *In* M. L. Prebble [ed.] Aerial control of forest insects in Canada. Thorn Press Ltd., Ottawa.

Marshall, T. L., J. L. Peppar, and E. J. Schofield. 1982. Prediction of 2SW and older Atlantic salmon returning to the Millbank trap, Miramichi River, New Brunswick. Canadian Atlantic Fisheries Scientific Advisory Committee, Research Document 82/51: 10 p.

May, A. W., and W. H. Lear. 1971. Digest of Canadian Atlantic salmon catch statistics. Fish. Res. Board Can. Tech. Rep. 270: 106 p.

McKenzie, R. A. 1959. Marine and freshwater fishes of the Miramichi River and estuary, New Brunswick, J. Fish. Res. Board Can. 16: 807–833.

1964. Smelt life history and fishery in the Miramichi River, New Brunswick. Bull. Fish. Res. Board Can. 144: 77 p.

Morry, C. J., and L. J. Cole. 1977. Limnology and fish populations of Red Indian Lake, a multi-use reservoir. Can. Fish. Mar. Serv. Tech. Rep. 691: 109 p.

O'Connell, M. F., and C. E. Bourgeois. 1987. Atlantic salmon enhancement on the Exploits River, Newfoundland, 1957–1984. N. Am. J. Fish. Manage. 7: 207–214.

O'Connell, M. F., J. P. Davis, and D. C. Scott. 1983. An assessment of the stocking of Atlantic salmon (*Salmo salar* L.) fry in the tributaries of the middle Exploits River, Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. 1225: 142 p.

O'Connell, M. F., J. B. Dempson, D. G. Reddin, and E. G. M. Ash. 1985. Status of Atlantic salmon (*Salmo salar* L.) stocks of the Newfoundland Region, 1984. Canadian Atlantic Fisheries Scientific Advisory Committee, Research Document 85/26: 58 p.

Paloheimo, J. E., and P. F. Elson. 1974. Reduction of Atlantic salmon (*Salmo salar*) catches in Canada attributed to the Greenland fishery. J. Fish. Res. Board Can. 31: 1467–1480.

Peppar, J. L., and E. J. Schofield. 1978. Juvenile Atlantic salmon densities, Miramichi River system, New Brunswick, 1969–77. Can. Fish. Mar. Serv. Data Rep. 91: 19 p.

Peterson, R. H. 1978. Physical characteristics of Atlantic salmon spawning gravel in some New Brunswick streams. Can. Fish. Mar. Serv. Tech. Rep. 785: 28 p.

Philpott, K. L. 1978. Miramichi channel study. Public Works Canada, Design and Construction Marine Directorate, Ottawa. 284 p.

Pippy, J. 1982. Report of the working group on the interception of mainland salmon in Newfoundland. Can. Man. Rep. Fish. Aquat. Sci. 1654: 187 p.

Porter, T. R. and D. J. Meerburg. 1977. Upwelling incubation boxes for Atlantic salmon (*Salmo salar*). Int. Counc. Explor. Sea CM 1977/M: 22: 13 p.

Randall, R. G. 1981. Production rate of juvenile Atlantic salmon (*Salmo salar* L.) in relation to available food in two Miramichi River, New Brunswick, nursery streams. Ph.D. thesis, University of New Brunswick, Fredericton, N.B. 218 p.

1982. Emergence, population densities and growth of salmon and trout fry in two New Brunswick streams. Can. J. Zool 60: 2239–2244.

1985. Spawning potential and spawning requirements of Atlantic salmon in the Miramichi River, New Brunswick. Canadian Atlantic Fisheries Scientific Advisory Committee, Research Document 85/68: 19 p.

Randall, R. G., and E. M. P. Chadwick. 1983. Assessment of the Miramichi River salmon stock in 1982. Canadian Atlantic Fisheries Scientific Advisory Committee, Research Document 83/21: 24 p.

1986. Density as a factor affecting the production of juvenile Atlantic salmon (*Salmo salar*) in the Miramichi and Restigouche rivers, New Brunswick. Pol. Arch. Hydrobiol. 33: 391–409.

Randall, R. G., and E. J. Schofield. 1987. Status of Atlantic salmon in the Miramichi River, 1986. Canadian Atlantic Fisheries Scientific Advisory Committee, Research Document 87/5: 32 p.

Randall, R. G., E. M. P. Chadwick, and E. J. Schofield. 1985. Status of Atlantic salmon in the Miramichi River, 1984. Canadian Atlantic Fisheries Scientific Advisory Committee, Research Document 85/2: 21 p.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191: 382 p.

Ruggles, C. P., and J. A. Ritter. 1980. Review of North American smolt tagging to assess the Atlantic salmon fishery off West Greenland. Rapp. P.-V. Réun. Cons. int. Explor. Mer 176: 82–92.

Ryan, P. M. 1984. Fyke net catches as indices of the abundance of brook trout, *Salvelinus fontinalis*, and Atlantic salmon, *Salmo salar*. Can. J. Fish. Aquat. Sci. 41: 377–380.

1986. Lake use by wild anadromous Atlantic salmon, *Salmo salar*, as an index of subsequent adult abundance. Can. J. Fish. Aquat. Sci. 43: 2–11.

Saunders, R. L. 1969. Contributions of salmon from the Northwest Miramichi River, New Brunswick, to various fisheries. J. Fish. Res. Board Can. 26: 269–278.

Scott, W. B. and E. J. Crossman. 1964. Fishes occurring in fresh waters of insular Newfoundland. Queen's Printer, Ottawa. 124 p.

1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

Shearer, W. M. 1961. Survival rate of young salmonids in streams stocked with green ova. Int. Counc. Explor. Sea CM/98. 3 p.

Smith, S. J. 1981. Atlantic salmon sport catch and effort data, Maritimes Region, 1951–1979. Can. Data Rep. Fish. Aquat. Sci. 258: 267 p.

Solomon, D. J. 1985. Salmon stock and recruitment, and stock enhancement. J. Fish. Biol. 27: 45–57.

Sturge, C. C. 1966. The Rattling Brook transfer 1957–65. Resource Development Branch, Newfoundland Region, St. John's. Prog. Rep. 41: 38 p.

1968. Production studies on the young stages of Atlantic salmon (*Salmo salar*) in an experimental area of Indian River Notre Dame Bay, Newfoundland. M.Sc. Thesis, Memorial Univ., St. John's, Nfld. 134 p.

Swetnam, D. A. B., and S. F. O'Neil. 1985. Collation of Atlantic salmon sport catch statistics, Maritime Provinces, 1960–69. Can. Data Rep. Fish. Aquat. Sci. 533: 289 p.

Symons, P. E. K. 1977. Dispersal and toxicity of the insecticide fenitrothion; predicting hazards of forest spraying. Residue Reviews 38: 1–36.

1979. Estimated escapement of Atlantic salmon (*Salmo salar*) for maximum smolt production in rivers of different productivity. J. Fish. Res. Board Can. 36: 132–140.

Taylor, V. R., and B. R. Bauld. 1973. A program for increased Atlantic salmon (*Salmo salar*) production on a major Newfoundland River. Int. Atl. Salmon Found. Spec. Public. Ser. 4: 339–347.

Welcomme, R. L. 1985. River fisheries. Food and Agricultural Organization of the United Nations. Fish. Tech. Pap. 262: 330 p.

Wilson, R. C. H. 1974. A report on the pollution of the Exploits River basin. Environmental Protection Service, Surveillance Rep. EPS 5-AR-74-3: 78 p.

Zippin, C. 1956. An evaluation of the removal method of estimating animal populations. Biometrics 12: 163–189.

Mississippi River Fisheries: A Case History

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Abstract

FREMLING, C. R., J. L. RASMUSSEN, R. E. SPARKS, S. P. COBB, C. F. BRYAN, AND T. O. CLAFLIN. 1989. Mississippi River fisheries: a case history, p. 309–351. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The Mississippi River (MR) is severely regulated, mainly for transportation and flood control. The Headwaters (HW) flow through 9 eutrophic and mesotrophic glacial lakes and 11 dams. Intensive channelization of the Upper Mississippi River (UMR) for navigation was begun in 1878, and the river is now routinely dredged. Broad, shallow impoundments were created on the UMR when 29 navigation dams were constructed during the 1930s to create a slack-water navigation channel 2.7–m deep between St. Louis, Missouri, and St. Paul, Minnesota. The Lower Mississippi River (LMR) has been channelized and shortened 229 km, but remains undammed; its natural floodplain has been decreased about 90 % by levee construction begun in 1727. The Atchafalaya River (AR), a major distributary and distinct ecological component, normally receives about 20 % of the discharge of the mainstem MR. MR backwaters are important fish production and nursery habitats, and most may be lost to sedimentation and eutrophication within 50 yr. Louisiana's coastal wetlands are critical to marine fishes and invertebrates, and about 0.6 % are being lost yearly to natural and human-induced forces, including levees which divert sediment directly into the Gulf of Mexico, instead of allowing it to build up the delta during annual floods. Although the supply of organic matter (OM) carried downsteam in the main channel exceeds requirements for secondary production within the river, the bulk of this OM may be recalcitrant and of little nutritional value to invertebrates and fish.

Distribution of 241 fish species reported from mainstem MR and AR has been influenced mainly by glaciation, natural barriers and human activities; species diversity generally increases downstream. Estimated annual UMR commercial fish harvest has ranged from 22.9 $kg \cdot ha^{-1}$ to 32.8 $kg \cdot ha^{-1}$ with standing stock estimates ranging as high as 1.035 $kg \cdot ha^{-1}$ in a tributary mouth of the Middle Mississippi River (MMR). Average standing stock in backwaters within the unleveed AR basin is 860 $kg \cdot ha^{-1}$. Annual harvest of sport fish on the UMR ranges from 15.9 $kg \cdot ha^{-1}$ in northern pools to 2.9 $kg \cdot ha^{-1}$ in southern pools. Throughout the MR and AR, sport fishing contributes much more to the economy than commercial fishing. A positive relation exists between area of inundated AR floodplain and commercial harvest of aquatic animals whose life spans approximate one year. There are fewer fishing regulations on the LMR and AR than on the HW, UMR, or MMR but they are considered adequate because the fishery apparently accomodates local demands. Recent environmental legislation requires mitigation for loss of fish and wildlife habitat, as well as rehabilitation of areas already degraded.

Résumé

FREMLING, C. R., J. L. RASMUSSEN, R. E. SPARKS, S. P. COBB, C. F. BRYAN, AND T. O. CLAFLIN. 1989. Mississippi River fisheries: a case history, p. 309–351. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Le fleuve Mississippi fait l'objet de mesures sévères de régularisation des eaux, notamment pour la circulation et le contrôle des crues. Les eaux supérieures traversent 9 lacs glaciaires eutrophes et mésotrophes et 11 barrages. La canalisation répétée du cours supérieur du Mississippi visant à permettre la navigation a débuté en 1878 et le fleuve est aujourd'hui dragué régulièrement. De larges bassins de retenue peu profonds ont été ménagés dans le cours supérieur du Mississippi, par suite de la construction de 29 barrages pour la navigation dans les années 1930 en vue de créer un canal de navigation à annulation périodique du courant de 2,7 m de profondeur entre St. Louis au Missouri et St. Paul au Minnesota. Le cours inférieur du Mississippi a été canalisé et raccourci de 229 km mais aucun barrage n'y a été construit; de plus, la superficie de sa plaine inondable a été réduite d'environ 90 % par la construction de digues commencée en 1727. La rivière Atchafalaya, un important défluent du Mississippi qui constitue un écosystème distinct, reçoit normalement 20 % environ du débit du bras principal du Mississippi. Les eaux dormantes du fleuve représentent d'importants habitats de production et de reproduction des poissons; la majeure partie de cette région pourrait bien disparaître d'ici 50 ans sous l'effet de la sédimentation et de l'eutrophisation. Les marais côtiers de la Louisiane ont une importance vitale pour les poissons et invertébrés marins; malheureusement, 0,6 % de ces marais disparaissent chaque année sous l'impact de forces naturelles et anthropiques, dont les digues qui forcent les sédiments à se déverser directement dans le golfe du Mexique au lieu de s'accumuler sur le delta durant les crues annuelles. Bien que la teneur en matières organiques de l'écoulement du chenal principal dépasse les exigences pour la production secondaire dans le fleuve, la majeure portion de ces matières organiques pourrait bien ne pas correspondre aux besoins nutritifs des invertébrés et des poissons.

La distribution des 241 espèces de poissons observées dans les bras principaux du Mississippi et de la rivière Atchafalaya reflète essentiellement la glaciation, les barrières naturelles et les activités de l'homme; la diversité des espèces augmente généralement vers l'aval. La récolte annuelle commerciale de poissons dans le cours supérieur de Mississippi varie, d'après des estimations, de 22,9 $kg \cdot ha^{-1}$ à 32,8 $kg \cdot ha^{-1}$ et le stock actuel atteint 1 035 $kg \cdot ha^{-1}$ dans l'embouchure d'un tributaire du cours moyen du Mississippi. Les stocks actuels moyens dans les eaux dormantes du bassin non endigué de la rivière Atchafalaya sont de 860 $kg \cdot ha^{-1}$. La récolte annuelle de poissons de sport dans le cours supérieur du Mississippi varie de 15,9 $kg \cdot ha^{-1}$dans les bassins plus au nord à 2,9 $kg \cdot ha^{-1}$ dans ceux du sud. Dans le Mississippi et la rivière Atchafalaya, la pèche sportive contribue beaucoup plus que la pêche commerciale à l'économie. Il existe une corrélation positive entre les zones inondées de la plaine de la rivière Atchafalaya et les récoltes commerciales d'animaux aquatiques dont la durée de vie est d'environ un an. Bien que les règlements sur la pèche sont moins nombreux pour le cours inférieur du Mississippi et la rivière Atchafalaya, que pour les eaux supérieures et les cours supérieurs et moyens du Mississippi, ils sont considérés comme étant adéquats puisque les produits de la pêche semblent répondre à la demande locale. Des lois récentes sur l'environnement prévoient des mesures visant à limiter la perte d'habitats de la faune et des poissons ainsi que la réhabilitation des régions déjà dégradées.

The Mississippi River (MR), the largest river in North America, flows 3 731 km from its source at Lake Itasca, Minnesota, to the Head-of-Passes, Louisiana (Fig. 1,2), where it splits into several distributaries (passes) and extends another 32 km to the Gulf of Mexico. It drains a basin of 4 759 049 km^2, about one-eighth the area of North America, including all or parts of 31 states and 2 Canadian provinces. The third longest river in the world, the MR has the second largest drainage basin and is the fifth largest river worldwide in average discharge (Keown et al. 1981).

Once vital to the exploration of North America and to the colonization and development of the United States, the MR has been intensively managed for flood control and for the transport of commercial cargoes over the past 200 yr. It is navigable upstream to Minneapolis for vessels of 2.7-m draft. The MR is flanked by flood-control levees or loessial escarpment from New Orleans to Dubuque and is impounded by a series of shallow navigation pools from St. Louis to Minneapolis.

For the purposes of this paper, the main stem of the MR is divided into four distinct ecological reaches: (1) Headwaters (HW) from its source (Lake Itasca) to St. Anthony Falls, (2) Upper Mississippi River (UMR) from St. Anthony Falls to the mouth of the Missouri River, (3) Middle Mississippi River (MMR) from the mouth of the Missouri River to the mouth of the Ohio River, and (4) Lower Mississippi River (LMR) from the mouth of the Ohio River to the Head-of-Passes. The Atchafalaya River (AR) (Fig. 2), a major distributary, is considered an additional ecological component of the MR. Locations along the main stem are given as river km above Head-of-Passes (RKM AHP). Important sites are mapped in Fig. 1 and 2.

Physical Features

Headwaters (HW)

The HW begins as a first-order stream (Strahler 1952) in the bogs and spruce swamps of northern Minnesota's Lake Itasca basin, a conifer-hardwood biome that lies within the Central Lowland physiographic province (Fenneman 1938). Originating as an outflow channel of Lake Itasca at 440 m above mean sea level (msl), the HW drops 204 m in its 824-km course through wetlands, wild rice beds, natural lakes, man-made impoundments, and several rapids to its southern limit at St. Anthony Falls (Fig. 3).

The course and character of the HW result from Wisconsin glaciation, which climaxed about 14 000 years before

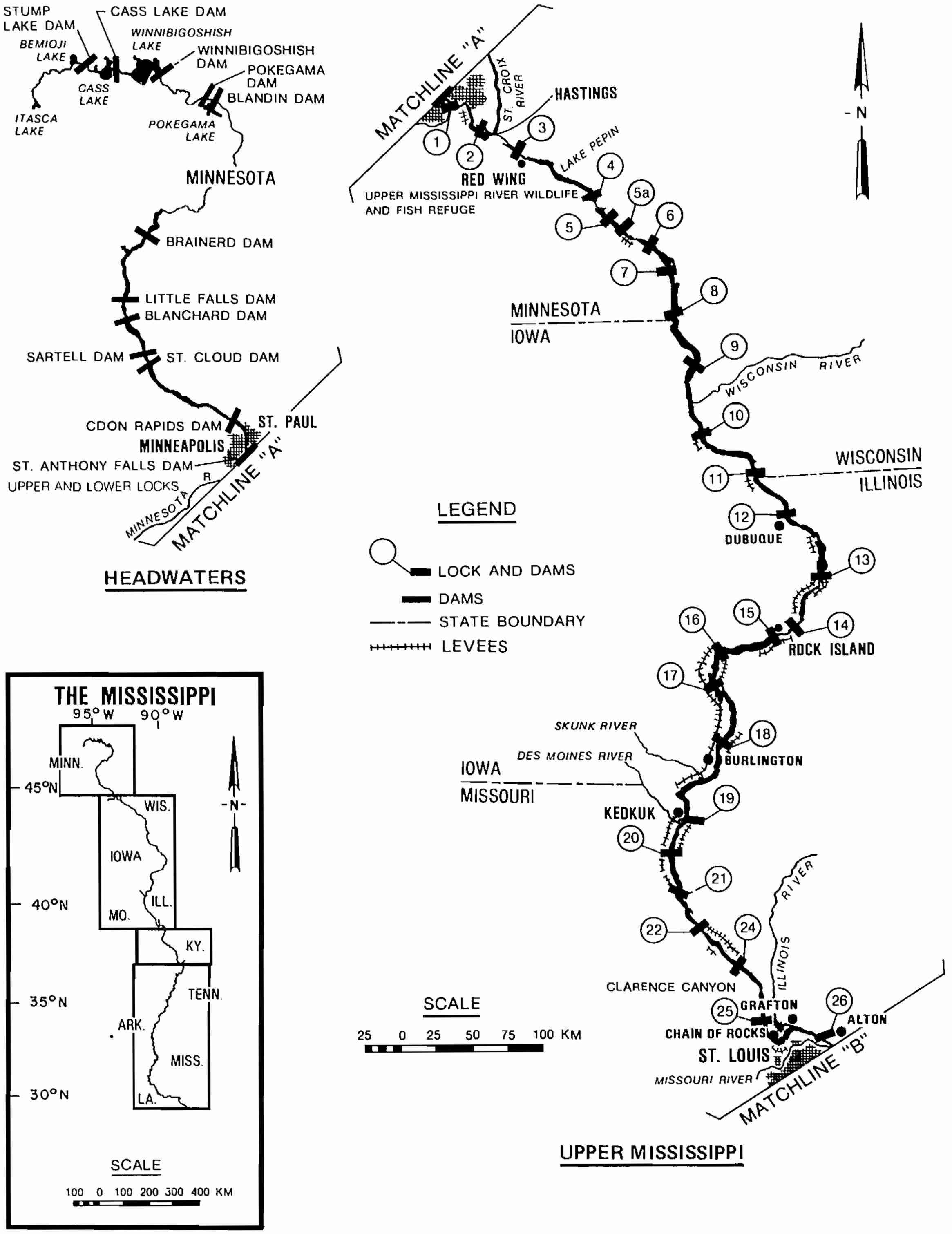

FIG. 1. Headwaters and Upper Mississippi River (USACE 1977, 1982). Technical assistance by C. H. Pennington, U.S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, MS.

present (B.P.). The HW flows alternately through sandplains, glacial lake beds, and moraine systems. Accordingly, its bed ranges from mud to gravel, boulders, and bedrock (Wright 1972a). St. Anthony Falls formed when the Glacial River Warren (Glacial Minnesota River) flowed over Platteville limestone and eroded the underlying St. Peter sandstone (Wright 1972b). The Falls subsequently retreated 26 km upstream, decreased in height from 23 to 12.2 m, and is presently protected by man-made reinforcements. Until locks were constructed, St. Anthony Falls was a formidable barrier to upstream movement of fish; for many years it was the head of navigation (Waters 1977).

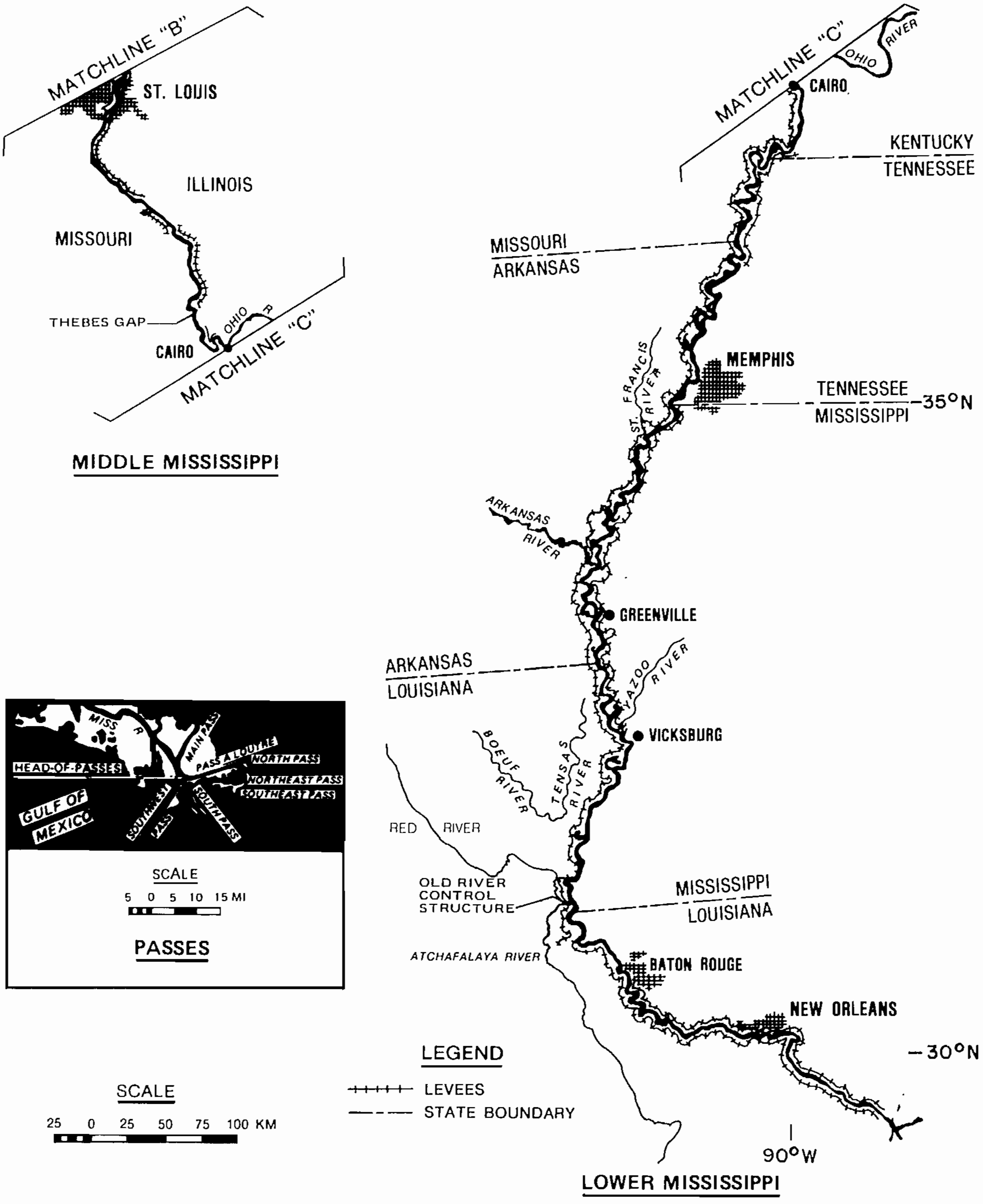

FIG. 2. Middle Mississippi, Lower Mississippi, and Atchafalaya rivers (USACE 1982, 1983). Technical assistance by C. H. Pennington, U.S. Army Corps of Engineers, Waterways Experiment Station, Vicksburg, MS.

Logging for white and Norway pine, begun in 1856, preceded farming in the northern HW area (Waters 1977). Virgin forests were gone by 1910, and diversified farming was marginally successful in cutover areas; hardwoods replaced pines in some areas. Major HW industries, in order of economic importance, are logging, recreation, and farming. The hundreds of lakes in the watershed are ringed with summer homes, resorts, and year-round residences. Farther downstream, farming and other industry become increasingly important.

Between Lake Itasca and Lake Winnibigoshish, the HW flows alternately as a low-gradient stream with boggy corridors and a high-gradient stream with forest corridors (Kucera and Peterson 1980). Stream slope in the upstream 700 km varies from 0.05 to 7.2 m•km^{-1} (Fig. 3) and sinuosity indices range from 1.03 to 4.5; the most sinuous reach occurs in the bed of Glacial Lake Aitkin in central Minnesota. Sediment discharge increases downstream as

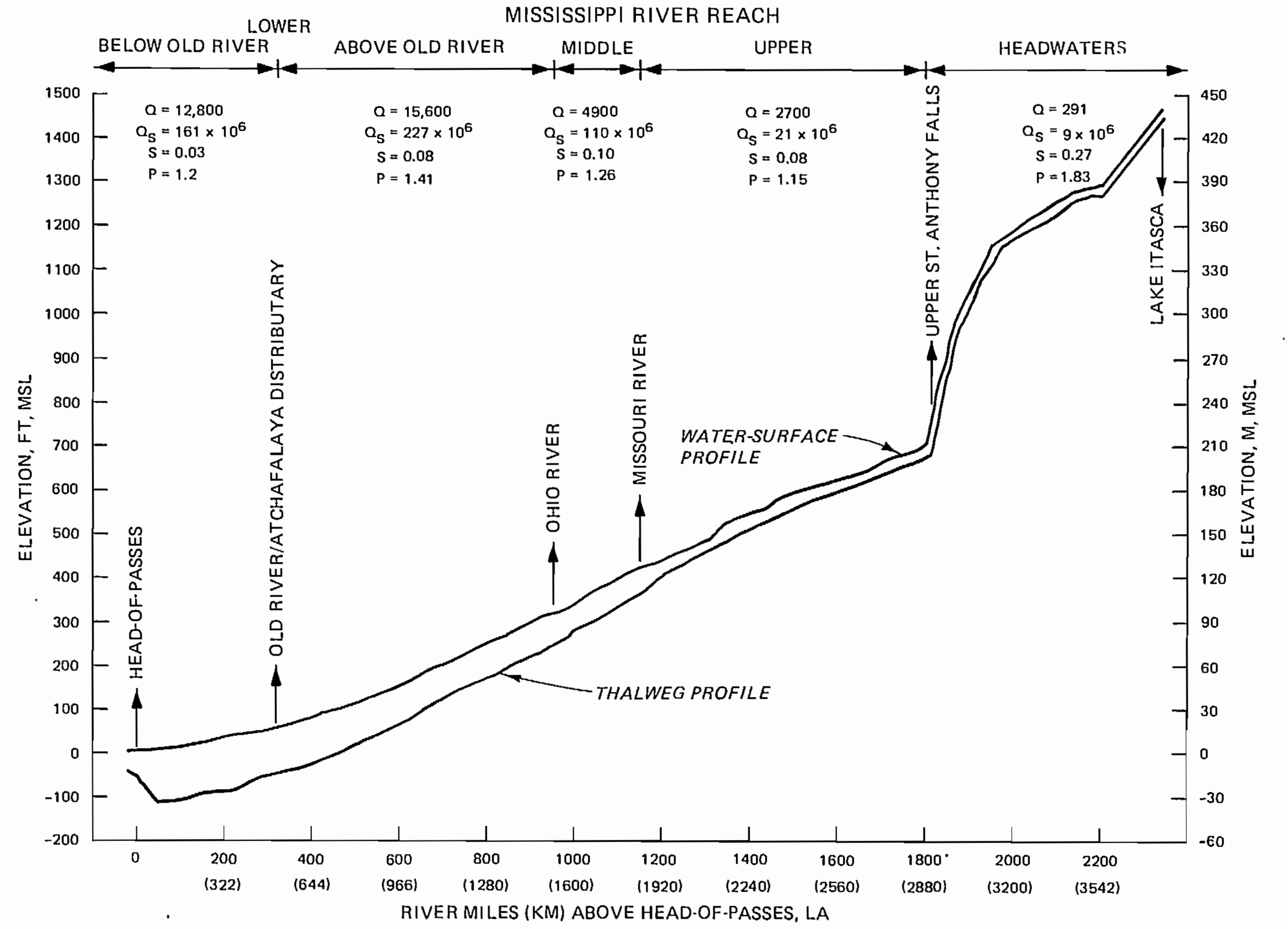

FIG. 3. Water surface and thalweg profiles for the Mississippi River. The water-surface profile is for a 10-yr return interval flow event. The thalweg profile is schematic and based on average river bottom elevations for reaches of various lengths depending on the availability of survey data. In-channel lakes in the headwaters reach, pools and crossings, and locks and dams are not indicated. Q = average water discharge, $m^3 \cdot S^{-1}$; Q_s = average total suspended sediment discharge, $t \cdot yr^{-1}$; S = water surface slope, $m \cdot km^{-1}$; P = sinuosity index. River kilometres are in parentheses. The thalweg profile above St. Anthony Falls is extremely variable due to flow through rapids, impoundments, and lakes.

forests give way to farmland. Sediment load has ranged from 19 140 to 4.3 $t \cdot day^{-1}$ (U.S. Geol. Sur. 1983a) at Anoka (Fig. 3). Depending on velocities, bed load material ranges from sand to gravel.

Eleven dams (Table 1) have replaced several falls and rapids. Nine in-channel glacial lakes are found in the HW (Table 2), including Lake Winnibigoshish and Lake Pokegama, both of which have been dammed as part of a U.S. Army Corps of Engineers (USACE) navigation and flood-control system that also includes 4 other reservoir lakes in the HW watershed. The 6 reservoirs have a combined drainage area of 11 746 km^2 and a total water-surface area of 1 007 km^2. Their original purpose was to store spring runoff in order to augment low summer flows for commercial navigation in the UMR between St. Paul and Prairie du Chien, but the 2.7-m channel dams of the 1930s made that function unnecessary. The HW reservoir dams are now used mainly for flood control, recreation, residential ammenities, conservation and related uses (USACE 1977). Erratic flow in the HW is a major factor limiting lotic communities. Low flows in late summer, for example, are exacerbated by reservoir storage at a time when river temperatures are at their maximum; the addition of waste heat from power plants, sewage, industrial waste, and agricultural runoff can cause unsatisfactory water quality conditions (Enblom 1977).

Since 1980, the upper 640 km of the HW have been under the purview of the Mississippi Headwaters Board, an eight-county tax-supported coalition with enforcement powers and comprehensive zoning ordinances (Goff et al. 1981).

Upper Mississippi River (UMR)

The UMR, a 9th- to 10th-order alluvial river (Strahler 1952), drains most of the Central Lowland physiographic province. It began its evolution about 500 000 years B.P. as an ice-marginal stream, incising its valley into sedimentary rocks as it flowed along the edge of the Nebraskan glacier. About 12 000 years B.P., the retreating late Wisconsin glacier blocked its own drainage into Hudson Bay, forming Glacial Lake Agassiz. For about 3 000 yr, high flows were maintained in the MR by overflows from Lake Agassiz via the Glacial River Warren and from Glacial Lake Superior via the St. Croix River. During this period, the

TABLE 1. Locks and/or Dams in Headwaters and Upper Mississippi River.

Name	Rkm[a]	Purpose	Date	Head[b] (m)	Owner
Stump Lake	3613.8	Hydroelec.	1908	8.2	Ottertail Power
Cass Lake	3588.5	Regul. lake level	1928	0.9	U.S. Forest Serv.
Winnibigoshish	3543.9	Reservoir	1891	5.1	COE[c]
Pokegama	3439.9	Reservoir	1884	2.9	COE
Blandin	3434.5	Pulp. stor.	1902	7.0	Blandin Paper
Brainerd	3150.1	Hydroelec.	1888	7.0	Potlatch
Little Falls	3088.1	Hydroelec.	1887	7.3	Minnesota Power
Blanchard	3073.8	Hydroelec.	1927	13.1	Minnesota Power
Sartell	3035.3	Hydroelec.	1904	5.9	Champion Intl.
St. Cloud	3025.5	Hydroelec.	1887	5.9	City
Coon Rapids	2928.8	Recreation	1906	6.1	County
Up. St. Anthony	2910.2	Navigation	1963	14.9	COE
Lo. St. Anthony	2909.6	Navigation	1956	8.2	COE
Lock & Dam 1	2900.3	Hydro/Nav	1917	11.5	Ford Co./COE[d]
Lock & Dam 2	2848.1	Navigation	1931	3.7	COE
Lock & Dam 3	2818.6	Navigation	1938	2.4	COE
Lock & Dam 4	2747.1	Navigation	1935	2.1	COE
Lock & Dam 5	2720.7	Navigation	1935	2.7	COE
Lock & Dam 5A	2708.5	Navigation	1936	1.7	COE
Lock & Dam 6	2685.6	Navigation	1936	2.0	COE
Lock & Dam 7	2666.6	Navigation	1937	2.4	COE
Lock & Dam 8	2629.1	Navigation	1937	3.3	COE
Lock & Dam 9	2578.7	Navigation	1937	2.7	COE
Lock & Dam 10	2525.9	Navigation	1937	2.4	COE
Lock & Dam 11	2474.2	Navigation	1937	3.3	COE
Lock & Dam 12	2431.9	Navigation	1939	2.7	COE
Lock & Dam 13	2376.8	Navigation	1939	3.3	COE
Lock & Dam 14	2329.8	Navigation	1939	3.3	COE
Lock & Dam 15	2313.1	Navigation	1934	4.8	COE
Lock & Dam 16	2271.7	Navigation	1937	2.7	COE
Lock & Dam 17	2239.3	Navigation	1939	2.4	COE
Lock & Dam 18	2196.5	Navigation	1937	3.0	COE
Lock & Dam 19	2122.0	Hydro/Nav	1913	11.6	Union Elec. Co/COE[e]
Lock & Dam 20	2088.2	Navigation	1936	3.0	COE
Lock & Dam 21	2058.7	Navigation	1938	3.2	COE
Lock & Dam 22	2020.6	Navigation	1938	3.1	COE
Lock & Dam 24	1975.8	Navigation	1940	4.5	COE
Lock & Dam 25	1924.3	Navigation	1938	4.5	COE
Lock & Dam 26	1862.3	Navigation	1938	7.3	COE[f]
Lock & Canal 27	1834.1	Navigation	1953	9.1	COE

[a] River km above Head-of-Passes.

[b] Head values for minimum flow.

[c] Corps of Engineers.

[d] New lock operational in 1931.

[e] Originally hydroelectric dam with 600-ft lock, 1200-ft lock added in 1958.

[f] To be replaced by new dam and 1200-ft lock to be operational in November, 1989. Construction of a second 600-ft lock was begun in 1988.

TABLE 2. Physical characteristics of lakes through which the HW flow sequentially. Data from Minnesota lake survey reports and personal communication with H. Latvala, D. Johnson, and D. Holmbeck of the Minnesota Dep. Nat. Resources.

	Area (km^2)	Littoral area(%)	Max. depth (m)	Mean depth (m)	Shoreline length (km)	Total alk. $\text{mg}\cdot\text{kg}^{-1}$	Trophic state
Itasca (source)	4.4	42	12.2	5.5	22.1	134	eutrophic
Irving	2.5	90	4.9	2.4	7.9	174	eutrophic
Bemidji	26.0	29	23.2	9.5	23.8	163	eutrophic
Stump	1.2	81	7.3	2.4	13.0	154	eutrophic
Big Wolf	4.3	34	17.7	8.5	11.9	160	eutrophic
Andrusia	6.2	28	18.3	7.9	15.0	158	eutrophic
Cass	63.1	20	36.6	7.6	62.8	157	eutrophic
Winnibigoshish	216.2	35	21.4	—	73.3	154	mesotrophic
Pokegama	26.8	30	34.2	—	70.5	109	mesotrophic

river incised deeply (as much as 90 m) into the valley.

As the glacier retreated northward, drainage was reestablished to the north and east, causing the flow from Lake Agassiz and Lake Superior to cease; consequently, the valley partially filled with glacial outwash sediments of sand and gravel (Simons et al. 1975). Valley filling continues today at a slow rate (Lane 1957). Terraces or remnants of ancestral floodplains presently flank the valley. Most of the UMR drainage basin is mantled with a thick layer of loess, the result of eolian transport of glacial materials prior to the development of extensive vegetation.

The alternating broad and narrow reaches of the present UMR reflect the structure of the gently dipping Paleozoic rocks into which it is incised. Broad reaches occur where softer sandstones have been eroded, leaving high bluffs of resistant rock; narrow reaches are found where resistant carbonate formations dip down to the river level (Wright 1972b; Hallberg et al. 1984).

The UMR drops only about 80 m as it flows 1 148 km from the foot of St. Anthony Falls to the confluence of the Missouri river (Fig. 3). Discharge is highly variable (Fig. 4), sediment load increases, and sinuosity decreases (Fig. 3).

Modification of the UMR and its watershed proceeded rapidly after the first steamboat travelled upstream to St. Anthony Falls in 1823. In 1824, the USACE began removing snags and sandbars, excavating rock to eliminate rapids, and damming sloughs to confine flows in the main channel (Fremling and Claflin 1984). These alterations enabled shallow-draft steamboats to use the river and its tributaries as water highways to the sea. Erosional processes in the watershed were accelerated as settlers logged the forests, grazed and plowed the prairies, and practiced steepland agriculture.

In 1878, the USACE began channelizing the river for navigation from the mouth of the Ohio River to Minneapolis by constructing wing dikes and revetments, closing side channels, and dredging. The wing dikes, constructed of rock and brush, extended outward like piers from the shore at right angles to the main channel and diverted flow into a single low-water channel, forcing the river to scour its channel to a minimum depth of 1.4 m. Between 1907 and 1912, additional channelization deepened the main channel to 1.8 m from the mouth of the Missouri River to Minneapolis.

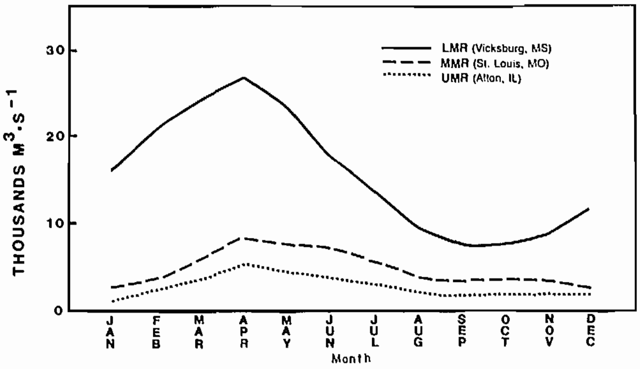

FIG. 4. Average monthly water discharge for the Lower Mississippi at Vicksburg, the Middle Mississippi at St. Louis, and the Upper Mississippi at Alton. Data based on daily gauge readings for 1930–75 (Tuttle and Pinner 1982).

A 2.7-m navigation channel with a minimum width of 121 m was achieved in the 1930s by a system of locks and dams (Table 1), by dredging, and by additional dike construction. Navigation dams transformed the free-flowing UMR into a series of shallow impoundments that occupy much of the river floodplain in the northern UMR reaches. The dams serve no flood control function. Only Lock and Dam (L&D) 1 and 19 presently produce electricity, but other hydropower projects are under consideration.

Navigation pools typically consist of three hydrological/ecological zones: (1) the tailwater reach downstream from a lock and dam, where open river conditions with wooded islands and deep sloughs are found; (2) the midpool reach, a transition area that contains flooded prairies and marshy areas; and (3) the downstream pool reach, where reservoir conditions prevail.

Middle Mississippi River (MMR)

The MMR traverses three physiographic provinces: the Central Lowlands, the Ozark Plateaus, and the Mississippi Embayment of the Gulf Coastal Plain. Downstream from St. Louis, the MMR floodplain extends about 160 km to Thebes Gap as a 5- to 7-km trench cut 120–150 m into Paleozoic bedrock. Limestone bluffs as high as 120 m form the valley walls. The river enters the Mississippi Embayment at Thebes Gap, a gorge cut through Shawneetown Ridge about 9 000 years B.P. The MMR floodplain then widens abruptly to about 80 km from Thebes Gap to the mouth of the Ohio River (Simons et al. 1975).

The MMR's modern course was established during late Wisconsin glaciation when the ancestral river was diverted near Rock Island from a segment of the Illinois River Valley to its present location. MMR meander belt position has been stable along the western valley wall for at least 200 yr. Meander scars on the flood plain indicate that the river was more mobile in the past.

The fluvial landscape of the MMR is principally the main channel, secondary channels, sandbars, islands and a few abandoned channels. The MMR has been extensively diked to maintain a 2.7-m navigation channel, and flood control levees have narrowed the floodplain. MMR surface area in 1968 was 260 km^2 (17 % islands, 83 % riverbed), 39 % less than in 1888 when the river was in a more natural state. The physical and limnological characteristics of the MMR are greatly influenced by the large input of sediment from the Missouri River.

The MMR flows 314 km from the mouth of the Missouri to the mouth of the Ohio. It is not markedly sinuous (Fig. 3), except in the reach located in the Mississippi Embayment, where the floodplain is comparatively wide. Top bank width of the MMR averages 975 m. The MMR receives about 60 % of its flow from the Mississippi basin and about 40 % from the Missouri basin. Maximum recorded discharge was 36 790 m$^3 \cdot s^{-1}$ in 1844; the minimum was 509 m$^3 \cdot s^{-1}$ in 1863. Annually, peak flow occurs in April and low flow in December (Fig. 4). Mean annual discharge has changed little in the past 110 yr, but the rating curve has shifted upward for all discharges greater than 8 490 m$^3 \cdot s^{-1}$ and has shifted downward for discharges below this level. Upward shift during high flow is at least partially a result of contraction of the high-water channel by dikes and loss of floodplain capacity due to leveeing and development. In case of low flows, the downward shift can be partially attributed to degradation of the low-water channel by wing dikes (Simons et al. 1975). River stage fluctuates as much as 15 m annually, effectively dewatering some secondary channels during low stages.

MMR sediment load has declined 66 % from pre-1935 levels, mainly due to sediment entrapment in Missouri River impoundments. The MMR presently receives about 80 % of its average suspended sediment load from the Missouri and about 20 % from the UMR (Tuttle and Pinner 1982). Suspended sediment load of the MMR at St. Louis averages 47 % clay, 38 % silt, and 15 % sand. Bed material is approximately 70 % medium-to-coarse sands (Keown et al. 1981).

Lower Mississippi River (LMR)

The LMR courses southward 1 570 km from the mouth of the Ohio River to the Gulf of Mexico and lies within the Central Gulf Coastal Plain physiographic province. A northward extending lobe of this province, known as the Mississippi Embayment, follows the axis of the Mississippi structural basin and comprises the northern part of the LMR valley (Schumm et al. 1982).

The southward-trending LMR and its valley are apparently a result of the derangement of continental drainage patterns following initiation of Nebraska glaciation, about 1.5 million years B.P. During the subsequent five cycles of continental glaciation and eustatic changes (100–200 m) in Gulf of Mexico surface levels, the valley enlarged progressively, degrading and filling alternately with glacial outwash sediments and alluviums. The ancestral LMR was a braided stream during waning glaciation, characterized by large inflows of glacial meltwater and sediments (Saucier 1974).

Subsequent to the climax of Wisconsin glaciation, the ancestral LMR began a gradual up-valley transformation from a braided to a meandering stream. By about 12 000 years B.P., a meandering regime was evident as far upstream as Baton Rouge and by 9 000 years B.P. as far upstream as Memphis. The river subsequently changed course from the basin's western to eastern lowlands due to diversion through Thebes Gap at the head of the LMR valley. Since then, the LMR has occupied five Holocene meander belts. It has occupied the present belt since about 2 800 years B.P. and exhibits a meandering regime throughout, except in the deltaic region south of New Orleans (Saucier 1974, 1981).

The natural floodplain of the extant river includes about 90 674 km^2 of the valley, which is approximately 1 060 km long and varies in width from 40 to 200 km (Fisk 1944). Natural floodways in the present meander belt (mainly the St. Francis, Yazoo and Bœuf-Tensas basins) historically carried excess floodwaters. Today, the floodplain subject to direct riverine overflow is reduced to approximately 10 120 km^2 by an extensive levee system.

Modification of the LMR began when the French constructed levees at New Orleans in 1727. By 1844, levees were continuous along the west bank northward to the Arkansas River and to Baton Rouge on the east bank. Much of the levee system deteriorated during the American Civil War in the 1860s, but work was resumed by the U.S. Mississippi River Commission (MRC) in 1882. To date, there are 3 532 km of levees, 2 587 km of which are main line levees. Levees have eliminated major natural floodways and reduced the land area of the floodplain by more than 90 %. Levee construction isolated many floodplain lakes and raised river flow lines; as a result 15 meander loops were severed between 1933 and 1942 to decrease stages. The cutoffs shortened the river 229 km, increased stream slope and current speed, and created several large floodplain lakes (Tuttle and Pinner 1982). Alignment of the channel has been stabilized by construction of about 1 368 km of revetment. Approximately 113 systems consisting of 331 km of dikes have been built upstream from RKM 515 AHP. The dike systems decrease width and increase depth of the main navigation channel at low flows, reduce divided flow conditions, adjust channel alignment, and increase channel stability. In spite of the levee system, the great 1973 flood inundated about 48 560 km^2.

Holocene alluvium of the river's modern leveed floodplain contains meander belts, backswamps, and deltaic plains (Fisk 1944; Saucier 1974). Meander belts contain abandoned channels (e.g., oxbow lakes), pointbars, and natural levees formed by lateral river migration. Backswamp areas are flood basins that border on and are lower than the natural meander belt and receive fine-grained suspended sediments from floodwaters.

The LMR is more sinuous than the MMR or UMR, with the most sinuous segment (SI 1.77) occurring in the 267-km reach downstream from the Old River Control Structure at RKM 515. Top bank width of the LMR averages 1 658 m; channel width at low flow (97 % exceedance discharge) averages 903 m (Tuttle and Pinner 1982). About 58 % of the average flow is from the Ohio River and about 38 % is from the MMR at their confluence. The annual LMR hydrograph is highly variable (Fig. 4); stage may fluctuate as much as 15 m in a given year. At the Old River Control Structure, about 20 % of mainstem discharge is diverted into the Atchafalaya (AR) distributary. At the Head-of-Passes the LMR channel diverges into five major distributary channels, which convey flow into the Gulf.

Average annual LMR suspended sediment load at Vicksburg is 280 390 t•yr^{-1} and has declined about 48 % since the 1960s. About 43 % of this suspended sediment comes from the MMR, about 31 % from the Ohio River, and the remainder from other tributary basins; approximately 37 % of the sediment load is diverted from the LMR into the AR distributary at the Old River Control Structure. Suspended sediment load contains 61 % silt–clay at Vicksburg. Bed material grades from coarse sands and gravel in the upper LMR reaches to fine sand, silt, and clay near the mouth (Keown et al. 1981).

Atchafalaya River (AR) and Estuarine Environments

About 400 years B.P., the AR became a natural LMR distributary when the same LMR meander loop receiving the Red River also intercepted the AR (Fig. 2). Log debris and sediments formed a plug, however, which prevented the AR from capturing LMR discharge. In 1831, excavation and debris removal began, causing the Old River meander loop to become a new connection between the LMR and the AR. Low-sill dams were built across the lower portion of the meander and across the Red River to direct excess flood water down the AR without stemming navigation between the LMR and the Red River. A navigation lock, completed in 1962, allows shallow draft navigation between the two rivers (Hebert 1967).

The AR, with a three-to-one advantage in bed slope over the LMR, has since become a principal distributary for the MR. Under natural conditions, the MR would probably have changed its route to the Gulf via the AR sometime between 1965 and 1975, thereby causing irreversible deterioration of the MR main stem downriver from Baton Rouge (Lower Miss. Reg. Compr. Study Coord. Comm. 1974). If this change had occurred, Baton Rouge, New Orleans, and other river cities might have lost their source of fresh water during periods of low flow; river transportation might have been curtailed; and flood-control and navigation structures could have been lost (Keown et. al 1981).

The Old River Control Structure, operational in 1963, prevents capture of the MR by the AR. An additional facility, the Auxilliary Structure, became operational in 1986. During normal flows, the AR drains 30 % of combined LMR and Red River flows to the Gulf; in terms of discharge it is the 6th largest North American river (Iseri and Langbein 1984). Its basin is North America's largest bottomland hardwood swamp (Glasgow and Noble 1974).

The 50 000-km^2 deltaic plain of the MR was formed during the past 8 000 years by a delta switching process whereby the river successively abandoned one delta site for another as it continuously found shorter paths to the Gulf of Mexico. The plain is dominated by an extensive network of distributary channels and natural levees that radiate outward from the MR main stem near Baton Rouge and extend southward into the Gulf (Frazier 1967; Penland and Boyd 1985). Normally, new deltas are created as abandoned ones are destroyed by wave action or currents. In recent years, however, this equilibrium has been altered, thereby jeopardizing Louisiana's coastal wetlands.

Louisiana's Coastal Zone contains 41 % of U.S. coastal wetlands and 25 % of all U.S. wetlands. It is one of the world's largest and richest estuarine areas, but its wetlands are being converted to open water or non-wetland habitats at the rate of over 130 $km^2 \cdot yr^{-1}$ (0.6 $\% \cdot yr^{-1}$) by natural and human-induced forces (Penland and Boyd 1985). Obvious human causes of accelerated wetland deterioration include inland movement of salt water via the intracoastal waterway, interception of alongshore sediment transport by jetties and seawalls, weakening of the barrier island profile by oil and gas pipelines and access canals, and pollution of many types. Especially critical is the erosion of Louisiana's barrier islands, which serve as the first line of defense against hurricane and tropical storm impacts and prevent destruction of freshwater swamps and marshes by the intrusion of salt water.

Rising relative sea levels (1.2–4.3 $cm \cdot yr^{-1}$) along the MR deltaic plain are apparently causing increased rates of transgression of delta complexes (Penland and Boyd 1985). About 20 % of the rise may be attributed to eustatic processes (e.g., global melting of ice caps), but 80 % may be caused by subsidence due mainly to normal compaction of sediments, but also to man's removal of water, oil, and natural gas.

Normal delta building processes are also being upset by human modifications of the sediment transport regimen. About 20 % of mainstem MR suspended sediment load is diverted to the AR. The remaining sediment is carried toward the Gulf but is impeded by an intrusive wedge of salt water that causes a portion of the sediment to settle out where it adversely affects navigation. Continued sediment deposition causes the 10.7-m contour at the mouth of the MR to advance seaward at about 30 $m \cdot yr^{-1}$ (Smith 1963). The input of sediment to shallow-water deltas has been curtailed by the closing of distributary channels (e.g., La Fourche River in 1904). Additional sediment is lost by directing it into the depths of the Gulf beyond the continental shelf via the LMR passes. Further, the suspended sediment load of the MR has decreased markedly in the last half century because of changing land-use practices and sediment storage in reservoirs of the MR watershed (Keown et al. 1981; Fremling 1988). At present, only the delta of the AR is growing; all others are degrading because of insufficient sediment input (Penland and Boyd 1985). Ironically, while upstream MR fishery habitats are being lost to sedimentation, decreased sedimentation in the delta area is causing the loss of nursery habitats and preventing the creation of new ones. LMR and AR estuarine environments are critical production areas for marine fishes and invertebrates. Indeed, they are the major reason that commercial landings in Louisiana currently account for 30 % of all U.S. landings (U.S. Dept. Comm. 1986).

Water Quality

In general terms, the MR discharges hard, slightly alkaline, nitrogen- and phosphorus-enriched water (Table 3). While hardness and alkalinity generally decrease downstream, nutrients increase until RKM 430 and then diminish to the mouth of the river. Nitrogen and phosphorus concentrations exceed generally accepted critical levels which, when combined with morphological, hydrological, and climatic factors, can lead to excessive primary productivity (Claflin et al. 1981), were it not for high turbidity, light attenuation, and turbulence (Bryan et al. 1974a).

Fluctuations in suspended sediments and nutrients from the watershed are generally associated with variations in discharge and with the proximity of monitoring stations to plumes of major tributaries. High spring runoff elevates concentrations of suspended solids, nitrogen, and phosphorus, particularly on the increasing limb of the spring flood. However, as spring floods progress, dilution causes suspended solids to diminish in the LMR (Everett 1971; Bryan et al. 1974a; Hartzog 1975; Wells 1980).

Suspended solids increase downstream, peaking at St. Louis due to the influence of the Missouri River (Table 3). From there, suspended solids gradually decrease downstream (except at Arkansas City where the White and Arkansas rivers cause an increase) to RKM 16 at Venice, Louisiana, where an additional 20 % of suspended solids settle out because of the river's approach to sea level (Wells 1980). The AR is usually higher in suspended solids than a comparable portion of the LMR because of high inflow from the Red River (Wells and Demas 1977).

Specific conductance generally increases downstream, reaching its peak at St. Louis due to the influence of the Missouri River. Increase in dissolved solids is caused primarily by sulfates and chlorides that enter the MR from western drainages (Platner 1946; Livingstone 1963). In the AR, during periods of low water in late summer and fall, sulfates and chlorides increase due to the overriding influence of the Red River and the brine wastes from oil exploration. The

TABLE 3. Water chemistry parameters (average and range) at representative sites along the Mississippi River and Atchafalaya River. Distances on the MR are upstream from Head-of-Passes; on the AR they are upstream from the point at which the river meets mean sea level.

Location and river km AHP or MSL	Specific conductance (μmhos•cm^{-1})	pH	Alkalinity (mg•L^{-1} as $CaCO_3$)	Hardness (mg•L^{-1} as $CaCO_3$)	Total phosphorus (mg•L^{-1} as P)	Ortho-phosphorus (mg•L^{-1} as P)	Nitrogen (NO_2 + NO_3) (mg•L^{-1} as N)	Nitrogen (amm. + org) (mg•L^{-1} as N)	Sus-pended sediments (mg•L^{-1})	Turbidity (NTU)
[a]Lake Itasca										
Outlet, MN	311	7.9	184	174	0.05	0.02	0.16	0.14	4.2	2.5
3710	(279-390)	(7.6-8.3)	(170-230)	(160-220)	(0.03-0.09)	(0.01-0.03)	(0.11-0.22)	(0.05-0.37)	(1.5-11.2)	(1.2-5.0)
[a]Stump Lake Dam, MN	301	8.2	178	176	0.07	0.03	0.13	0.13	7.0	2.1
3592	(270-370)	(8.0-8.3)	(150-210)	(150-200)	(0.05-0.10)	(0.01-0.06)	(0.11-0.23)	(0.32-1.12)	(2.1-11.1)	(1.2-4.2)
[a]St. Paul. MN	380	8.3	165	220	0.13	0.11	2.60	0.90	18.0	6.6
2904	(330-495)	(8.1-8.8)	(123-171)	(150-240)	(0.10-0.15)	(0.05-0.12)	(0.11-0.33)	(0.60-1.50)	(7.0-25.0)	(4.4-7.0)
[a]Keokuk, IA	410	7.9	155	195	0.28	0.12	3.40	1.00	240.0	34.0
2122	(365-515)	(7.3-8.1)	(139-186)	(180-250)	(0.15-0.47)	(0.08-1.50)	(1.10-5.70)	(0.90-2.90)	(31-418)	(10-74)
[b]St. Louis. MO	495	7.8	156	200	0.51	0.82	2.90	2.90	340.0	97.0
1832	(373-628)	(7.6-8.3)	(114-193)	(160-240)	(0.18-0.80)	(0.05-0.11)	(1.20-4.00)	(1.10-5.00)	(92-596)	(19-300)
[c]Memphis, TN	385	7.8	103	148	0.38	0.24	1.35	1.10	259.0	86.0
1183	(270-500)	(7.4-8.5)	(67-140)	(96-200)	(0.10-0.67)	(0.04-0.44)	(0.70-3.00)	(0.10-2.10)	(24-495)	(2-170)
[c]Arkansas City, AR	422	7.8	105	142	0.31	0.20	1.31	1.31	283.0	70.0
891	(295-550)	(7.5-8.4)	(66-143)	(74-210)	(0.07-0.54)	(0.04-0.35)	(0.73-2.90)	(0.31-2.30)	(35-532)	(1-140)
[d]St. Francisville, LA	410	7.9	109	162	0.53	0.22	0.68	0.98	250.0	163.0
430	(155-645)	(7.3-8.5)	(23-190)	(85-320)	(0.00-4.70)	(0.00-4.70)	(0.20-7.90)	(0.00-2.43)	(150-1200)	(28-360)
[e]Atchafalaya River										
Mellville, LA	385	7.4	105	144	0.15	0.09	1.20	0.76	297.0	85.0
188	(176-699)	(6.6-8.1)	(48-142)	(60-190)	(0.08-0.33)	(0.02-0.24)	(0.30-2.60)	(0.30-3.40)	(90-844)	(9-190)
[b]New Orleans, LA	445	7.5	101	162	0.21	0.12	1.90	0.60	190.0	67.0
161	(338-528)	(6.9-8.1)	(87-121)	(130-190)	(0.17-0.38)	(0.09-0.19)	(0.06-2.30)	(0.40-0.80)	(43-377)	(4-80)
[f]Atchafalaya River	356	7.2	122	138	0.22	0.13	0.90	1.70	260.0	85.0
Morgan City, LA	(182-694)	(6.5-8.2)	(25-180)	(89-190)	(0.04-0.72)	(0.00-0.32)	(0.20-2.20)	(0.40-7.50)	(16-904)	(4-220)

[a] U.S. Geological Survey 1983a.

[b] U.S. Geological Survey 1983b.

[c] U.S. Geological Survey 1983c.

[d] Everett (1971), Bryan et al. (1974a).

[e] Wells and Demas (1977), Carlson et al. (1982, 1983, 1984).

[f] Bryan et al. (1974b, 1975), Bryan and Sabins (1978), Holland et al. (1983b), Carlson et al. (1982, 1983, 1984).

AR takes on the character of the MR during the remainder of the year, since most of its discharge is MR water.

Other impacts on water quality can be observed in the pooled reaches of the UMR downstream from urban areas. For example, treated sewage from Minneapolis/St. Paul enters the UMR approximately 56 km upstream from Lake Pepin, a natural river impoundment created by the Chippewa River delta. Lake Pepin serves as a settling basin for pollutants and has become enriched with nutrients and heavy metal contaminants (Bailey and Rada 1984) and polychlorinated biphenyls (PCBs) (Mauck and Olson 1977). In pooled UMR reaches there are additional inputs of autochthonous nitrogen and phosphorus from backwater areas.

Among three LMR stations (main channel, abandoned channel, and dike field at RKM 504–566) during low flow, Sabol et al.(1984) found the main channel to be highest in nitrite-nitrate nitrogen, total phosphorus, dissolved orthophosphorus, turbidity, and detritus; the abandoned channel was lowest for these paramenters. Highest chlorophyll-*a* concentrations and zooplankton densities occurred in the abandoned channel. During flood conditions, physical, chemical, and biological parameters were similar in all three habitats. Water quality within dike fields was variable, depending on whether lentic or lotic conditions prevailed. During low flow, thermal stratification and hypolimnetic anoxia may occur in abandoned channels and pools within dike fields (Sabol et al. 1984; Beckett and Pennington 1986).

Fish Fauna

Distribution

Common and scientific names, distribution, relative abundance, and current status of MR fish species are listed in Table 4. Distribution maps and basic biological information on fishes of North America have been compiled by Lee et al. (1980). Of the 260 truly freshwater species respresenting 13 families in the entire MR basin (Hocutt and Wiley 1986), 195 species in the main stem of the MR and AR comprise nearly one-third of the approximately 600 freshwater fishes known in North America (Moyle and Cech 1982). When saltwater or anadromous forms are included, the complexity grows by 46 species included in 19 families and 37 genera, all of which are reported only from the LMR and AR basins. A general downstream increase in diversity occurs with 67 taxa found in the HW, 132 in the five UMR

TABLE 4. Distribution and relative abundance of Mississippi River fish species by reach (Eddy and Underhill 1974; Rasmussen 1979; Van Vooren 1983; U.S. Fish and Wildlife Service 1985; Moyle 1975; Les 1979; Roosa 1977; Natural Land Institute 1981; Nordstrom et. al. 1977; Hatcher no date; Sutton 1986; Kelly 1965; Robins et al. 1980; Beckett and Pennington 1986; Bryan et al. 1974b, 1975, 1976; Conner 1982; Guillory 1982; Grady et al. 1983)[a]. Reaches have been delineated and abbreviated as follows: Headwater Lakes (HWL); Headwater Reach (HWR); St. Anthony Falls to Pool 4 (UMR-1); Pools 5–10 (UMR-2); Pools 11–15 (UMR-3); Pools 16–19 (UMR-4); Pools 20–26 (UMR-5); Middle River (MMR); Cairo to New Orleans (LMR-1); New Orleans to Head-of-Passes (LMR-2).

Family species[b]	Reach										Atchafalaya River
	HWL	HWR	UMR-1	UMR-2	UMR-3	UMR-4	UMR-5	MMR	LMR-1	LMR-2	
Petromyzontidae											
Chestnut lamprey (*Ichthyomyzon castaneus*) [IA,KY][c]			R	R	U	U	O	O			X
Southern brook lamprey (*Ichthyomyzon gagei*)									X	X	X
Silver lamprey (*Ichthyomyzon unicuspis*)			O	O	O	O	U	U	X	X	X
Carcharhinidae											
Bull shark (*Carcharhinus leucas*)							H			?	X
Dasyatidae											
Atlantic stingray (*Dasyatis sabina*)										?	X
Bluntnose stingray (*Dasyatis sayi*)										X	X
Acipenseridae											
Lake sturgeon (*Acipencer fulvescens*) [MN,WI,IA,IL,MO,TN,KY]			U	R	R	R	R	R			
Atlantic sturgeon (*Acipenser oxyrhynchus*)									R	R	R
Pallid sturgeon (*Scaphirhynchus albus*) [IA,MO,KY]							R	R	R	R	R
Shovelnose sturgeon (*Scaphirhynchus platorynchus*)			O	O	O	O	O	O	C	O	C
Polyodontidae											
Paddlefish (*Polyodon spathula*) [MN,WI,KY]			R	R	O	O	O	O	O	O	O
Lepisosteidae											
Spotted gar (*Lepisosteus oculatus*)							U	R	C	O	C
Longnose gar (*Lepisoteus osseus*)	O		C	C	C	C	C	O	C	C	R
Shortnose gar (*Lepisosteus platostomus*)		H	C	C	C	C	C	A	O	C	R
Alligator gar (*Lepisosteus spatula*)[IL,MO,KY,TN]							R	R	O	U	C
Amidae											
Bowfin (*Amia calva*)	O	O	C	C	C	C	C	O	C	O	C
Elopidae											
Ladyfish (*Elops saurus*)										X	X
Tarpon (*Megalops atlanticus*)										?	X
Anguillidae											
American eel (*Anguilla rostrata*)[WI]		H	O	O	U	U	O	U	U	U	U
Ophichthidae											
Speckled worm eel (*Myrophis punctatus*)											X

TABLE 4. (cont'd) Distribution and relative abundance of Mississippi River fish species by reach (Eddy and Underhill 1974; Rasmussen 1979; Van Vooren 1983; U.S. Fish and Wildlife Service 1985; Moyle 1975; Les 1979; Roosa 1977; Natural Land Institute 1981; Nordstrom et. al. 1977; Hatcher no date; Sutton 1986; Kelly 1965; Robins et al. 1980; Beckett and Pennington 1986; Bryan et al. 1974b, 1975, 1976; Conner 1982; Guillory 1982; Grady et al. 1983)[a]. Reaches have been delineated and abbreviated as follows: Headwater Lakes (HWL); Headwater Reach (HWR); St. Anthony Falls to Pool 4 (UMR-1); Pools 5–10 (UMR-2); Pools 11–15 (UMR-3); Pools 16–19 (UMR-4); Pools 20–26 (UMR-5); Middle River (MMR); Cairo to New Orleans (LMR-1); New Orleans to Head-of-Passes (LMR-2).

Family species[b]	Reach										Atchafalaya River
	HWL	HWR	UMR-1	UMR-2	UMR-3	UMR-4	UMR-5	MMR	LMR-1	LMR-2	
Clupeidae											
Alabama shad (*Alosa alabamae*)[IA,MO,KY]								R	H	H	O
Skipjack herring (*Alosa chrysochloris*)]MN,WI,IA]			R	R	R	H	O	U	C	C	C
Gulf menhaden (*Brevoortia patronus*)										C	A
Gizzard shad (*Dorosoma cepedianum*)		A	A	A	A	A	A	A	A	A	A
Threadfin shad (*Dorosoma petenense*)							U	U	A	A	A
Engraulidae											
Bay anchovy (*Anchoa mitchilli*)										A	A
Hiodontidae											
Goldeye (*Hiodon alosoides*) [WI]	A	A	U	U	R	U	O	O	O	C	C
Mooneye (*Hiodon tergisus*)			C	C	C	C	O	U	R	R	?
Salmonidae											
Cisco (*Coregonus artedii*) [IL]	C										
Lake whitefish (*Coregonus clupeaformis*) [IL]	C										
Rainbow trout (*Salmo gairdneri*)		X	X	X	X					X	X
Brown trout (*Salmo trutta*)		X	X	X	X						
Brook trout (*Salvelinus fontinalis*)		X	X	X	X						
Osmeridae											
Rainbow smelt (*Osmerus mordax*)								X	X	X	?
Umbridae											
Central Mudminnow (*Umbra limi*)[AR,KY]	A	C		X	X				X		
Esocidae											
Grass pickerel (*Esox americanus vermiculatus*)[IA]				X	R	X	X	X	X	X	C
Northern pike (*Esox lucius*)	C	C	C	C	C	O	O	X			
Muskellunge (*Esox masquinongy*)	O	U	X	X							
Chain pickerel (*Esox niger*) [KY]									X	X	U
Cyprinidae											
Central stoneroller (*Campostoma anomalum*)		O	X	X	X	X	X	X	X	X	X
Goldfish (*Carassius auratus*)		X		X	X	X	X	X	U	U	U
Common carp (*Cyprinus carpio*)	O	C	A	A	A	A	A	A	A	A	A
Grass carp (*Ctenopharyngodon idella*)				R	X	X	X	U	U	U	U
Silverjaw minnow (*Ericymba buccata*)[TN]								X	X	X	X

TABLE 4. (cont'd) Distribution and relative abundance of Mississippi River fish species by reach (Eddy and Underhill 1974; Rasmussen 1979; Van Vooren 1983; U.S. Fish and Wildlife Service 1985; Moyle 1975; Les 1979; Roosa 1977; Natural Land Institute 1981; Nordstrom et. al. 1977; Hatcher no date; Sutton 1986; Kelly 1965; Robins et al. 1980; Beckett and Pennington 1986; Bryan et al. 1974b, 1975, 1976; Conner 1982; Guillory 1982; Grady et al. 1983)[a]. Reaches have been delineated and abbreviated as follows: Headwater Lakes (HWL); Headwater Reach (HWR); St. Anthony Falls to Pool 4 (UMR-1); Pools 5–10 (UMR-2); Pools 11–15 (UMR-3); Pools 16–19 (UMR-4); Pools 20–26 (UMR-5); Middle River (MMR); Cairo to New Orleans (LMR-1); New Orleans to Head-of-Passes (LMR-2).

Family species[b]	Reach										Atchafalaya River
	HWL	HWR	UMR-1	UMR-2	UMR-3	UMR-4	UMR-5	MMR	LMR-1	LMR-2	
Western silvery minnow (*Hybognathus argyritis*)							X	R	R		
Brassy minnow (*Hybognathus hankinsoni*)		O	U	O							
Cypress minnow (*Hybognathus hayi*)[KY]									R	R	R
Mississippi silvery minnow (*Hybognathus nuchalis*)		U	U	U	U		U	R	C	C	C
Plains minnow (*Hybognathus placitus*)[KY]								U	R		R
Speckled chub (*Hybopsis aestivalis*)[WI]			C	C	C	C	C	C	C	C	C
Clear chub (*Hybopsis winchelli*)									C	C	?
Sturgeon chub (*Hybopsis gelida*)[IA,MO,KY]							R	R			
Flathead chub (*Hybopsis gracilis*)[KY]					R		O	R			
Sicklefin chub (*Hybopsis meeki*)[IA,MO,KY]								R	R	R	?
Silver chub (*Hybopsis storeriana*)			C	C	C	C	C	C	C	O	C
Gravel chub (*Hybopsis x-punctata*)[WI,IA,KY]								R			
Hornyhead chub (*Nocomis biguttatus*)[KY]	O	O	C								
Bluehead chub (*Nocomis leptocephalus*)									X	X	?
Golden shiner (*Notemigonus crysoleucas*)	O	O	O	O	O	O	O	U	U	U	C
Pallid shiner (*Notropis amnis*)[WI,MO,KY]			H	R	R		H		R	R	R
Pugnose shiner (*Notropis anogenus*)[MN,WI,IA,IL]			X	X							
Emerald shiner (*Notropis atherinoides*)	A	A	A	A	A	A	A	A	A	A	A
Blackspot shiner (*Notropis atrocaudalis*)											C
Red River shiner (*Notropis bairdi*)											U
River shiner (*Notropis blennius*)			A	A	A	A	A	C	A	A	A
Bigeye shiner (*Notropis boops*)						X	X	X	X	O	O
Ghost shiner (*Notropis buchanani*)[WI]			H	H	R	C	C	O	R	R	U
Bluntface shiner (*Notropis camurus*)[KY]									X		
Ironcolor shiner (*Notropis chalybaeus*)									X	X	X
Striped shiner (*Notropis chrysocephalus*)[WI]								X	X	X	X
Common shiner (*Notropis cornutus*)	A	A	O	O	R	R	R				
Bigmouth shiner (*Notropis dorsalis*)	O	O	O	O	O	O	O	X			
Pugnose minnow (*Notropis emiliae*)[WI,IA,MO]			R	R	R	U		H	U	R	U

TABLE 4. (cont'd) Distribution and relative abundance of Mississippi River fish species by reach (Eddy and Underhill 1974; Rasmussen 1979; Van Vooren 1983; U.S. Fish and Wildlife Service 1985; Moyle 1975; Les 1979; Roosa 1977; Natural Land Institute 1981; Nordstrom et. al. 1977; Hatcher no date; Sutton 1986; Kelly 1965; Robins et al. 1980; Beckett and Pennington 1986; Bryan et al. 1974b, 1975, 1976; Conner 1982; Guillory 1982; Grady et al. 1983)[a]. Reaches have been delineated and abbreviated as follows: Headwater Lakes (HWL); Headwater Reach (HWR); St. Anthony Falls to Pool 4 (UMR-1); Pools 5–10 (UMR-2); Pools 11–15 (UMR-3); Pools 16–19 (UMR-4); Pools 20–26 (UMR-5); Middle River (MMR); Cairo to New Orleans (LMR-1); New Orleans to Head-of-Passes (LMR-2).

Family species[b]	Reach										Atchafalaya River
	HWL	HWR	UMR-1	UMR-2	UMR-3	UMR-4	UMR-5	MMR	LMR-1	LMR-2	
Ribbon shiner (*Notropis fumeus*)									X	X	X
Blackchin shiner (*Notropis heterodon*)	A	C	O								
Blacksnose shiner (*Notropis heterolepis*)[IA,IL,MO]	A	O	R								
Bluehead shiner (*Notropis hubbsi*)											X
Spottail shiner (*Notropis hudsonius*)[KY]	C	C	C	C	C	C	C	R		R	
Longnose shiner (*Notropis longirostris*)									U	U	O
Red shiner (*Notropis lutrensis*) [WI]					U	C	C	C	O	O	O
Taillight shiner (*Notropis maculatus*)[ky]									O	R	X
Ozark minnow (*Notropis nubilus*)[WI]			O					X			
Chub shiner (*Notropis potteri*)									H	H	X
Rosyface shiner (*Notropis rubellus*)			O	R	R						?
Silverband shiner (*Notropis shumardi*)[IA]					R		O	O	A	C	A
Spotfin shiner (*Notropis spilopterus*)		C	C	C	C	C	O	X			
Sand shiner (*Notropis stramineus*)		O	O	O	O	O	O	U	X		X
Weed shiner (*Notropis texanus*)[WI,IA]			U	U	U				U	U	U
Redfin shiner (*Notropis umbratilis*)[WI]			O	O	X	X			X	X	U
Blacktail shiner (*Notropis venustus*)[KY]								X	C	C	C
Mimic shiner (*Notropis volucellus*)	A	O	O	O				O	C	C	C
Steelcolor shiner (*Notropis whipplei*)									X	R	R
Suckermouth minnow (*Phenacobius mirabilis*)				H	U	U	U	O			U
Northern redbelly dace (*Phoxinus eos*)	C	C									
Southern redbelly dace (*Phoxinus erythrogaster*)					X						U
Finescale dace (*Phoxinus neogaeus*)		O									
Bluntnose minnow (*Pimephales notatus*)	C	O	O	O	O	O	O	O	O	O	C
Fathead minnow (*Pimephales promelas*)	C	U	U	U	U	U	U	R	R	R	U
Slim minnow (*Pimephales tenellus*)											U
Bullhead minnow (*Pimephales vigilax*)			A	A	A	A	A	C	U	U	U
Blacknose dace (*Rhinichthys atratulus*)	O	C		X	X						
Creek chub (*Semotilus atromaculatus*)	O	O	X	X	X		X		X	X	X
Pearl dace (*Semotilus margarita*)[IA]	O	O	X		X						

TABLE 4. (cont'd) Distribution and relative abundance of Mississippi River fish species by reach (Eddy and Underhill 1974; Rasmussen 1979; Van Vooren 1983; U.S. Fish and Wildlife Service 1985; Moyle 1975; Les 1979; Roosa 1977; Natural Land Institute 1981; Nordstrom et. al. 1977; Hatcher no date; Sutton 1986; Kelly 1965; Robins et al. 1980; Beckett and Pennington 1986; Bryan et al. 1974b, 1975, 1976; Conner 1982; Guillory 1982; Grady et al. 1983)[a]. Reaches have been delineated and abbreviated as follows: Headwater Lakes (HWL); Headwater Reach (HWR); St. Anthony Falls to Pool 4 (UMR-1); Pools 5–10 (UMR-2); Pools 11–15 (UMR-3); Pools 16–19 (UMR-4); Pools 20–26 (UMR-5); Middle River (MMR); Cairo to New Orleans (LMR-1); New Orleans to Head-of-Passes (LMR-2).

Family species[b]	Reach										Atchafalaya River
	HWL	HWR	UMR-1	UMR-2	UMR-3	UMR-4	UMR-5	MMR	LMR-1	LMR-2	
margarita)[IA]	O	O	X		X						
Catostomidae											
River carpsucker (*Carpiodes carpio*)			O	C	C	C	C	A	A	A	A
Quillback (*Carpiodes cyprinus*)		O	C	C	C	C	C	U	U	U	U
Highfin carpsucker (*Carpiodes velifer*)			O	O	O	U	O	X	U	U	
White sucker (*Catostomus commersoni*)	C	C	C	C	X	X	X	X			
Blue sucker (*Cycleptus elongatus*)[MN,WI,KY,TN]			U	R	U	U	U	R	O	O	O
Creek chubsucker (*Erimyzon oblongus*)									U	U	U
Lake chubsucker (*Erimyzon succetta*)									U	U	U
Northern hog sucker (*Hypentelium nigricans*)			R	R	R	X		X	X	X	X
Smallmouth buffalo (*Ictiobus bubalus*)			O	O	C	C	C	O	A	C	C
Bigmouth buffalo (*Ictiobus cyprinellus*)	H	O	C	C	C	C	C	C	C	O	O
Black buffalo (*Ictiobus niger*)[WI,KY]			H	R	R	U	U	O	U	U	U
Spotted sucker (*Minytrema melanops*)			O	C	O	U			U	U	U
Silver redhorse (*Moxostoma anisurum*)		C	O	O	R	R	U	X			
River redhorse (*Moxostoma carinatum*)[WI,IA]			R	R	R			R			
Golden redhorse (*Moxostoma erythrurum*)			U	O	U	R	R	X			
Shorthead redhorse (*Moxostoma macrolepidotum*)	C	C	C	C	C	O	O	U			
Blacktail redhorse (*Moxostoma poecilurum*)									X	X	X
Greater redhorse (*Moxostoma valenciennesi*)[WI]		R		R	R						
Ictaluridae											
White catfish (*Ictalurus catus*)					X			X			
Blue catfish (*Ictalurus furcatus*)[MN,WI]			H		H	H	O	O	A	A	A
Black bullhead (*Ictalurus melas*)	C	O	O	O	O	O	O	U	X	C	C
Yellow bullhead (*Ictalurus natalis*)	O	O	O	O	O	O	O	U	R	R	R
Brown bullhead (*Ictalurus nebulosus*)[MO]	C	C	O	O	R	R	R	X	X	X	R
Channel catfish (*Ictalurus punctatus*)			C	C	C	C	C	C	A	A	A
Mountain madtom (*Noturus eleutherus*)									X		X
Stonecat (*Noturus flavus*)			H	U	U	U	O	O	R	R	
Tadpole madtom (*Noturus gyrinus*)	C	O	O	O	O	U	U	U	R	R	R
Speckled madtom (*Noturus leptacanthus*)										X	?

TABLE 4. (cont'd) Distribution and relative abundance of Mississippi River fish species by reach (Eddy and Underhill 1974; Rasmussen 1979; Van Vooren 1983; U.S. Fish and Wildlife Service 1985; Moyle 1975; Les 1979; Roosa 1977; Natural Land Institute 1981; Nordstrom et. al. 1977; Hatcher no date; Sutton 1986; Kelly 1965; Robins et al. 1980; Beckett and Pennington 1986; Bryan et al. 1974b, 1975, 1976; Conner 1982; Guillory 1982; Grady et al. 1983)[a]. Reaches have been delineated and abbreviated as follows: Headwater Lakes (HWL); Headwater Reach (HWR); St. Anthony Falls to Pool 4 (UMR-1); Pools 5–10 (UMR-2); Pools 11–15 (UMR-3); Pools 16–19 (UMR-4); Pools 20–26 (UMR-5); Middle River (MMR); Cairo to New Orleans (LMR-1); New Orleans to Head-of-Passes (LMR-2).

Family	Reach										Atchafalaya
species[b]	HWL	HWR	UMR-1	UMR-2	UMR-3	UMR-4	UMR-5	MMR	LMR-1	LMR-2	River
Freckled madtom (*Noturus nocturnus*)							U		X	X	R
Brown madtom (*Noturus phaeus*)										X	?
Northern madtom (*Noturus stigmosus*)									X	?	?
Flathead catfish (*Pylodictis olivaris*)			C	C	O	O	C	C	A	A	A
Ariidae											
Hardhead catfish (*Arius felis*)										O	O
Gafftopsail catfish (*Bagre marinus*)										X	X
Aphredoderidae											
Pirate perch (*Aphredoderus sayanus*)[WI,IA]				U	H	H			R	R	U
Percopsidae											
Trout-perch (*Percopsis omiscomaycus*)[KY]	C	A	O	O	U	U	U	H			
Gadidae											
Burbot (*Lota lota*)[IA,MO,KY]	O	O	O	U	R	R	R	R			
Belonidae											
Atlantic needlefish (*Strongylura marina*)										O	O
Cyprinodontidae											
Sheepshead minnow (*Cyprinodon variegatus*)										U	U
Northern studfish (*Fundulus catenatus*)								X	X	X	X
Golden topminnow (*Fundulus chrysotus*)									X	X	C
Gulf killifish (*Fundulus grandis*)										O	O
Saltmarsh topminnow (*Fundulus jenkinsi*)										R	?
Blackstripe topminnow (*Fundulus notatus*)						O	O	O	O	O	U
Starhead topminnow (*Fundulus notti*)[WI,IA,KY]							X		X	X	?
Blackspotted topminnow (*Fundulus olivaceus*)								X	X	X	U
Rainwater killifish (*Lucania parva*)									U	U	U
Poeciliidae											
Mosquitofish (*Gambusia affinis*)					R	R	C	O	O	O	A
Least killifish (*Heterandria formosa*)									O	O	O
Sailfin molly (*Poecilia latipinna*)										?	U

TABLE 4. (cont'd) Distribution and relative abundance of Mississippi River fish species by reach (Eddy and Underhill 1974; Rasmussen 1979; Van Vooren 1983; U.S. Fish and Wildlife Service 1985; Moyle 1975; Les 1979; Roosa 1977; Natural Land Institute 1981; Nordstrom et. al. 1977; Hatcher no date; Sutton 1986; Kelly 1965; Robins et al. 1980; Beckett and Pennington 1986; Bryan et al. 1974b, 1975, 1976; Conner 1982; Guillory 1982; Grady et al. 1983)[a]. Reaches have been delineated and abbreviated as follows: Headwater Lakes (HWL); Headwater Reach (HWR); St. Anthony Falls to Pool 4 (UMR-1); Pools 5–10 (UMR-2); Pools 11–15 (UMR-3); Pools 16–19 (UMR-4); Pools 20–26 (UMR-5); Middle River (MMR); Cairo to New Orleans (LMR-1); New Orleans to Head-of-Passes (LMR-2).

Family species[b]	Reach										Atchafalaya River
	HWL	HWR	UMR-1	UMR-2	UMR-3	UMR-4	UMR-5	MMR	LMR-1	LMR-2	
Atherinidae											
Brook silverside (*Labidesthes sicculus*)	C	C	C	C	C	O	O	U	U	U	U
Rough silverside (*Membras martinica*)										X	?
Inland silverside (*Menidia beryllina*)[KY]								R	A	A	A
Tidewater silverside (*Menidia peninsulae*)										X	?
Gasterosteidae											
Brook stickleback (*Culaea inconstans*)	O	X	X								
Ninespine stickleback (*Pungitius pungitius*)	O										
Syngnathidae											
Gulf pipefish (*Syngnathus scovelli*)										U	U
Percichthyidae											
White bass (*Morone chrysops*)			C	C	C	C	C	C	A	C	A
Yellow bass (*Morone mississipiensis*)			H	O	U	U	O	R	O	C	C
Striped bass (*Morone saxatilis*)								X	O	O	O
Centrarchidae											
Shadow bass (*Ambloplites ariommus*)									X	X	R
Rock bass (*Ambloplites rupestris*)	C	C	C	C	R	R	R				
Flier (*Centrarchus macropterus*)								X	X	X	O
Banded pygmy sunfish (*Elassoma zonatum*)									X	X	O
Green sunfish (*Lepomis cyanellus*)	O	O	O	O	O	O	O	U	U	U	U
Pumpkinseed (*Lepomis gibbosus*)[MO]	O	O	O	C	C	U					
Warmouth (*Lepomis gulosus*)			H	U	U	O	O	U	U	U	A
Orangespotted sunfish (*Lepomis humilis*)			O	O	C	C	C	U	U	U	C
Bluegill (*Lepomis macrochirus*)	A	A	A	A	A	A	A	C	A	C	A
Dollar sunfish (*Lepomis marginatus*)										X	O
Longear sunfish (*Lepomis megalotis*)[WI,IA]							X	X	C	U	U
Redear sunfish (*Lepomis microlophus*)							X	X	U	U	C
Spotted sunfish (*Lepomis punctatus*)										?	O
Bantam sunfish (*Lepomis symmetricus*)										X	O
Smallmouth bass (*Micropterus dolomieui*)	O	C	O	O	U	U	U	X	X		?
Spotted bass (*Micropterus punctulatus*)								R	U	U	O

TABLE 4. (cont'd) Distribution and relative abundance of Mississippi River fish species by reach (Eddy and Underhill 1974; Rasmussen 1979; Van Vooren 1983; U.S. Fish and Wildlife Service 1985; Moyle 1975; Les 1979; Roosa 1977; Natural Land Institute 1981; Nordstrom et. al. 1977; Hatcher no date; Sutton 1986; Kelly 1965; Robins et al. 1980; Beckett and Pennington 1986; Bryan et al. 1974b, 1975, 1976; Conner 1982; Guillory 1982; Grady et al. 1983)[a]. Reaches have been delineated and abbreviated as follows: Headwater Lakes (HWL); Headwater Reach (HWR); St. Anthony Falls to Pool 4 (UMR-1); Pools 5–10 (UMR-2); Pools 11–15 (UMR-3); Pools 16–19 (UMR-4); Pools 20–26 (UMR-5); Middle River (MMR); Cairo to New Orleans (LMR-1); New Orleans to Head-of-Passes (LMR-2).

Family species[b]	Reach										Atchafalaya River
	HWL	HWR	UMR-1	UMR-2	UMR-3	UMR-4	UMR-5	MMR	LMR-1	LMR-2	
Largemouth bass (*Micropterus salmoides*)	A	C	C	C	C	C	C	O	C	O	A
White crappie (*Pomoxis annularis*)		U	C	C	C	C	C	C	C	O	C
Black crappie (*Pomoxis nigromaculatus*)	C	C	C	C	C	C	C	O	U	U	A
Percidae											
Crystal darter (*Ammocrypta asprella*)[WI,IA,KY]				R	H				X	X	U
Western sand darter (*Ammocrypta clara*)[IA,KY]			O	O	O	O	O	H	X	X	U
Scaly sand darter *Ammocrypta vivax*)[KY]									X	X	U
Mud darter (*Etheostoma asprigene*)[WI,IA]			H	R	R			R	R	R	O
Rainbow darter (*Etheostoma caeruleum*)				R			X		R	?	?
Bluntnose darter (*Etheostoma chlorosomum*)[WI,IA]				H				X	U	U	U
Iowa darter (*Etheostoma exile*)				X							
Fantail darter (*Etheostoma flabellare*)			X	X	H		X	X			
Swamp darter (*Etheostoma fusiforme*)									U	X	O
Slough darter (*Etheostoma gracile*)									U	X	O
Least darter (*Etheostoma microperca*)[MN,WI,IA,KY]	A	A									
Johnny darter (*Etheostoma nigrum*)[KY]		U	U	U	U	U	U	X	X	X	?
Goldstripe darter (*Etheostoma parvipinne*)										X	O
Cypress darter(*Etheostoma proeliare*)										X	O
Orangethroat darter (*Etheostoma spectabile*)[IA]							X	X			X
Gulf darter (*Etheostoma swaini*)										?	
Redfin darter (*Etheostoma whipplei*)										X	X
Banded darter (*Etheostoma zonale*)[KY]				X	X				X	X	O
Yellow perch (*Perca flavescens*)	A	C	C	C	O	O	H				
Logperch (*Percina caprodes*)	A	A	C	C	C	O	O	O	U	U	U
Channel darter (*Percina copelandi*)											U
Gilt darter (*Percina evides*)[WI,IA,KY]				H							
Blackside darter (*Percina maculata*)			X	X			X		X	X	X
Saddleback darter (*Percina ouachitae*)									U		
Slenderhead darter (*Percina phoxocephala*)			H	R	R	R	R	R			
Dusky darter (*Percina sciera*)								X	X	X	X
River darter (*Percina*											

TABLE 4. (cont'd) Distribution and relative abundance of Mississippi River fish species by reach (Eddy and Underhill 1974; Rasmussen 1979; Van Vooren 1983; U.S. Fish and Wildlife Service 1985; Moyle 1975; Les 1979; Roosa 1977; Natural Land Institute 1981; Nordstrom et. al. 1977; Hatcher no date; Sutton 1986; Kelly 1965; Robins et al. 1980; Beckett and Pennington 1986; Bryan et al. 1974b, 1975, 1976; Conner 1982; Guillory 1982; Grady et al. 1983)[a]. Reaches have been delineated and abbreviated as follows: Headwater Lakes (HWL); Headwater Reach (HWR); St. Anthony Falls to Pool 4 (UMR-1); Pools 5–10 (UMR-2); Pools 11–15 (UMR-3); Pools 16–19 (UMR-4); Pools 20–26 (UMR-5); Middle River (MMR); Cairo to New Orleans (LMR-1); New Orleans to Head-of-Passes (LMR-2).

Family species[b]	Reach										Atchafalaya River
	HWL	HWR	UMR-1	UMR-2	UMR-3	UMR-4	UMR-5	MMR	LMR-1	LMR-2	
shumardi)			C	C	C	C	C	O	U	U	X
Stargazing darter *Percina uranidea*)										U	X
Sauger (*Stizostedion canadense*)			C	C	C	C	C	C	O	O	?
Walleye (*Stizostedion vitreum vitreum*)	A	C	C	C	C	C	O	U	R		
Carangidae											
Crevalle jack (*Caranx hippos*)										X	X
Horse-eye jack (*Caranx latus*)										X	X
Leather jacket (*Oligoplites saurus*)										X	X
Lutjanidae											
Gray snapper (*Lutjanus griseus*)										?	X
Gerreidae											
Yellowfin mojarra (*Gerres cinereus*)										X	X
Sparidae											
Sheepshead (*Archosargus probatocephalus*)										O	X
Pinfish (*Lagodon rhomboides*)										O	X
Sciaenidae											
Freshwater drum (*Aplodinotus grunniens*)	U		C	C	C	C	A	A	A	A	A
Silver perch (*Bairdiella chrysoura*)										O	O
Sand seatrout (*Cynoscion arenarius*)										X	C
Spotted seatrout (*Cynoscion nebulosus*)										O	C
Silver seatrout (*Cynoscion nothus*)										X	X
Spot (*Leiostomus xanthurus*)										X	C
Gulf kingfish (*Menticirrhus littoralis*)										O	C
Atlantic croaker (*Micropogonias undulatus*)										O	C
Black drum (*Pogonias cromis*)										X	C
Red drum (*Sciaenops ocellatus*)										O	C
Cichlidae											
Mozambique tilapia (*Tilapia mossambica*)										X	X
Mugilidae											
Striped mullet (*Mugil cephalus*)									O	C	A
White mullet (*Mugil curema*)										?	?
Eleotridae											
Fat sleeper (*Dormitator											

TABLE 4. (cont'd) Distribution and relative abundance of Mississippi River fish species by reach (Eddy and Underhill 1974; Rasmussen 1979; Van Vooren 1983; U.S. Fish and Wildlife Service 1985; Moyle 1975; Les 1979; Roosa 1977; Natural Land Institute 1981; Nordstrom et. al. 1977; Hatcher no date; Sutton 1986; Kelly 1965; Robins et al. 1980; Beckett and Pennington 1986; Bryan et al. 1974b, 1975, 1976; Conner 1982; Guillory 1982; Grady et al. 1983)[a]. Reaches have been delineated and abbreviated as follows: Headwater Lakes (HWL); Headwater Reach (HWR); St. Anthony Falls to Pool 4 (UMR-1); Pools 5–10 (UMR-2); Pools 11–15 (UMR-3); Pools 16–19 (UMR-4); Pools 20–26 (UMR-5); Middle River (MMR); Cairo to New Orleans (LMR-1); New Orleans to Head-of-Passes (LMR-2).

Family species[b]	Reach										Atchafalaya River
	HWL	HWR	UMR-1	UMR-2	UMR-3	UMR-4	UMR-5	MMR	LMR-1	LMR-2	
maculatus)										O	X
Spinycheek sleeper (*Eleotris pisonis*)										O	X
Gobiidae											
Lyre goby (*Evorthodus lyricus*)										X	X
Violet goby (*Gobioides broussoneti*)										O	X
Darter goby (*Gobionellus boleosoma*)										O	X
Sharptail goby (*Gobionellus hastatus*)										X	X
Freshwater goby (*Gobionellus shufeldti*)										?	X
Spottail goby (*Gobionellus stigmaturus*)										O	X
Naked goby (*Gobiosoma bosci*)										O	X
Clown goby (*Microgobius gulosus*)										O	X
Scombridae											
Spanish mackerel (*Scomberomorus maculatus*)										X	X
Cottidae											
Mottled sculpin (*Cottus bairdi*)	C	O									
Banded sculpin (*Cottus carolinae*)							X				
Bothidae											
Bay wiff (*Citharichthys spilopterus*)										O	X
Fringed flounder (*Etropus crossotus*)										X	X
Southern flounder (*Paralichthys lethostigma*)										C	C
Soleidae											
Lined sole (*Achirus lineatus*)										X	X
Hogchoker (*Trinectes maculatus*)										O	C
Cynoglossidae											
Blackcheek tonguefish (*Symphurus plagiusa*)										X	X
Total Number of Species	49	62	99	106	105	86	98	114	134	174	180
Total Number of Species Minus Strays (X)	49	57	88	91	90	78	83	82	94	114	125

[a] In addition to the references cited, the following individuals reviewed and provided input to the table from their unpublished works: Ronald Benjamin, Wis. Dept. Natural Resources, Courthouse, Alma, WI 54601; David A. Etnier, Zool. Dept., Univ. Tenn., Knoxville, TN 37916; Gordon Farabee, Mo. Dept. Cons., 323 S. Main, Palmyra, MO 63461; Larry Gates and Gary Grunwald, Area Fish. Hdqtrs., Minn. Dept. Natural Resources, Lake City, MN 55041; James Holzer and Pamela Thiel, Wis. Dept. Natural Resources, 3550 Mormon Coulee Rd., 108 State Office Bldg., LaCrosse, WI 54601; Donny R. Lowery, Tenn. Valley Auth., Room 10, E and D Bldg., Muscle Shoals, AL 35660; Gary Lucas, Miss. Dept.Wildl. Cons., P.O. Box 451, Jackson, MS 39205-0451; John R. MacGregor, Ky. Dept. Fish & Wildl. Resources, Arnold L. Mitchell Bldg., #1 Game Farm Road, Frankfort, KY 40601; William L. Pflieger, Fish & Wildl.

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[b] Key to the status of a species:

? — Status unknown (not counted as present in total number of species).

X — Probably occurs only as a stray from a tributary, inland stocking, or salt water.

H — Records of occurrence are available, but no collections have been documented in the last ten years.

R — Considered to be rare. Some species in this category may be on the verge of extirpation.

U — Uncommon, does not usually appear in sample collections; populations are small, but species in this category do not appear to be on the verge of extirpation.

O — Occasionally collected, not generally distributed, but local concentrations may occur.

C — Commonly taken in most sample collections; makes up a large portion of some samples.

A — Abundantly taken in all river surveys.

[c] Species listed by the Federal Government or any state as extinct, extirpated, endangered, threatened, protected, of special concern, or on a watch list are noted according to the listing authority as follows: F — Federal, MN — Minnesota, WI —Wisconsin, IA — Iowa, IL — Illinois, MO — Missouri, KY — Kentucky, TN — Tennessee, AR — Arkansas, MS — Mississippi, LA — Louisiana.

reaches, 114 in the MMR, and about 150 in the LMR and AR. Most of the 21 ubiquitous forms are representatives of "old" ichthyofaunas (Miller 1965) of pre-, and early-Tertiary origin, such as the sturgeons, gars, bowfin, goldeye, a few cyprinids, a few ictiobine suckers, bullheads, crappies, and two larger percids. The less widely dispersed species represent "new" adaptively-radiating post-Miocene faunas and include the shiners, moxostomine suckers, madtoms, top-minnows, sculpins, small (Estheostomini) darters, and lepomine sunfishes (Jenkins et al. 1972). Other than the commercially exploited lake sturgeon and paddlefish, rare species are found primarily among the "new" faunas whose habitats are threatened by human activities. Most salmonids and esocids, numerous minnows and shiners, two redhorses, the burbot, and several percids are "cold- or cool-water" forms. Aside from the euryhaline taxa, diversity in the lower reaches is enriched by 2 clupeids, the chain pickerel, 13 cyprinids, 1 redhorse, 4 madtoms, several topminnows, 1 atherinid, 4 centrarchids and 7 darters.

UMR fish assemblages have been influenced by at least four periods of glaciation, three major tributaries (Ohio, Missouri, and Illinois rivers), natural barriers, channelization and development for commercial navigation, pollution, and the introduction of exotic species.

Glaciation undoubtedly played a role in altering HW and UMR fish communities. Because of the River's north–south axis, however, many species probably retreated ahead of the southward-moving glaciers and repopulated northern reaches as the glaciers receded (Hynes 1970).

Until modern times, St. Anthony Falls prevented colonization of the HW reach by 59 of the 123 fish species known to have occurred originally in the UMR and contiguous waters below the falls (Eddy et al. 1963). Original fish fauna above the falls included mostly lake species that were able to cross drainage divides at times of flood or when glacial lakes connected the HW with the St. Croix River and the Red River of the North (Underhill 1957). Evidence that the river was formerly connected with Hudson Bay drainage via Glacial Lake Agassiz is provided by distribution of the freshwater drum, which ranges from the Gulf of Mexico up the MR to St. Anthony Falls but is common in the Minnesota River and in the Red River of the North all the way to Hudson Bay, apparently having the greatest latitudinal range of any North American freshwater fish (Fremling 1980). Presence of the cold water burbot in northern UMR and HW reaches provides evidence of the river's former connection with the Hudson Bay drainage to the north via Glacial Lake Agassiz.

Completion of the locks at St. Anthony Falls in 1963 provided access for all species previously excluded from the HW, and the dam at Coon Rapids, completed in 1906, is now the principal migration barrier and serves to maintain distinct fish communities in the UMR and HW. The St. Cloud dam, 64.4 km upstream, is an additional migration barrier (Enblom 1977). Channel catfish have been stocked above the falls; carp and freshwater drum were probably introduced accidentally.

UMR navigation and hydropower (L&D 19) dams were considered by Coker (1913, 1930) to be barriers to migration of fish, especially skipjack herring. Recent evidence (Holland et al. 1984) supports Coker's views but establishes that some species do migrate through L & D 19 and other UMR navigation dams. Pflieger (1975) and Smith (1979) suggested that the dams may have blocked lake sturgeon spawning movements; however, the length of the sturgeon's immature life (18–20 yr) and its susceptibility to nets and boat propellors have also been important to its decline. The same may be true for paddlefish, which frequently swim near the surface and therefore seem especially vulnerable to propellors.

Anoxic zones have also served as barriers to fish movement. L&D 1, completed in 1917, collected most of the raw sewage of Minneapolis and St. Paul. L&D 2, completed in 1930 at Hastings, accumulated the remainder of the Metro sewage and that of the suburbs, packing houses, and stockyards. The Bureau of Fisheries reported that during August of 1927, 73 km of the river below St. Paul lacked sufficient oxygen to sustain fish life of any kind. Although navigation dams did not cause the pollution problem, they exacerbated the situation and focused attention on the deteriorating quality of the water. A sewage treatment system built in 1938 improved water quality, and most fish species could again live in the reach below St. Paul (Scarpino 1985).

Generally, the number of fish species can be expected to increase from a river's source to its mouth (Hynes 1970). This relationship generally holds true in the MR; there are about 2.5 times as many species in LMR-1 and LMR-2 than in the HW with an intermediate number in the UMR and MMR (Table 4). However, the relationship between river length, river order, and species diversity is not linear. Diversity increases downriver from the HW through subreach UMR-3, declines in UMR-4, remains about the same through the MMR, and then increases in the LMR. A greater diversity may be expected in subreaches UMR-3 and UMR-4 because they appear to be a transition zone between the northern and southern fish faunas. However, development of the flood plain, leveeing, industrialization, and other perturbations increase in these subreaches, and continue in downstream reaches. These more southern reaches also lack the influence of cold tributaries, and species diversity is apparently adversely affected by decreased habitat diversity (Smith et al. 1971; Pflieger 1975). The MMR, influenced by both the Illinois and Missouri rivers, is extensively channelized and leveed, and shows a lower species diversity (114 species) than the UMR (132 species). Thirty-two of the MMR species are not considered river residents, but strays from tributaries or the result of inland stocking. Introduced exotics in the MMR include common carp, rainbow smelt, goldfish, grass carp, and striped bass.

The fish community of the LMR differs from that of the UMR or the MMR because of the influences of UMR dams, the Missouri and the Ohio rivers, and the Gulf of Mexico. Numbers of shovelnose sturgeon, blue sucker, and blue catfish in the UMR have declined in recent years (Pflieger 1975). These three species appear to be present in sizable numbers in swift current habitats of the LMR (Pennington et al. 1980). The Missouri River exerts a strong influence on MMR fish fauna, and the Ohio strongly affects LMR fish composition (Smith 1979). The Missouri contributes a number of species to the MR which are restricted to and are regular components of MMR fish populations. Among these species are pallid sturgeon, western silvery minnow, plains minnow, sturgeon chub, flathead chub and sicklefin chub. The influence of the Missouri River is also seen in the distribution of such species as walleye and sauger. The walleye, less tolerant of turbidity and sediment than the sauger, is not common below the Mississippi's confluence with the more heavily silt-laden Missouri. Near the mouth of the Ohio River, such species as skipjack herring, threadfin shad, silverband shiner, mimic shiner, and inland silverside increase. LMR species diversity is increased by at least 46 marine species that may occur as far upstream as St. Francisville, Louisiana, during low flow when the intrusion of a wedge of salt water occurs.

A few ubiquitous species are abundant or occur commonly throughout the entire river: gizzard shad, emerald shiner, and bluegill. Several others are abundant or common in all reaches downstream below the HW: longnose gar, shortnose gar, bowfin, common carp, silver chub, river shiner, bigmouth buffalo, channel catfish, flathead catfish (except in UMR-4 and 5), white bass, largemouth bass, white crappie, freshwater drum, and river carpsuckers. Present in significant numbers only in the headwaters are the goldeye, cisco, lake whitefish, central mudminnow, common shiner, blackchin shiner, blacknose shiner, northern redbelly dace, bluntnose minnow, fathead minnow, blacknose dace, silver redhorse, black bullhead, brown bullhead, tadpole madtom, trout-perch, least darter, and mottled sculpin. Some species are abundant or common only in the UMR or MMR, including the mooneye, ghost shiner, golden shiner, red shiner, bullhead minnow, quillback carpsucker, mosquitofish, pumpkinseed, orangespotted sunfish, river darter, and sauger. Threadfin shad, silverband shiner, smallmouth buffalo, blue catfish, inland silverside, striped mullet, and skipjack herring are abundant only in the LMR.

Fish Assemblages by Habitat Type

Headwaters (HW)

HW habitat types are typical of those found in large temperate streams, but also include those of in-channel glacial lakes. The most abundant large fishes in the HW reach between Lake Itasca and Lake Winnibigoshish are white sucker, rock bass, and yellow perch. The most abundant forage species are bigmouth and common shiners. Sport fishing is limited to a low density northern pike fishery. Limiting factors include unstable substrate, minimal gradient, boggy corridors, areas of dense aquatic vegetative growth, and periodic subminimal flows (Kucera and Peterson 1980). Because resource exploitation has been minimal, the upper HW reach has maintained its ecological integrity; fish communities are apparently about the same as they were in the late 1800s.

Flowing waters of the middle HW reach contain 31 fish species with redhorse, white sucker, northern pike, and yellow perch predominating; northern pike, pumpkinseed, bluegill, and black crappie are dominant in lentic areas. Natural reproduction is adequate, but carrying capacity is low (Johnson 1968).

The lower HW reach contains 40 fish species, predominantly carp, smallmouth bass, and shorthead redhorse. Smallmouth bass and walleye, both of which spawn successfully, are the main game fishes. During the last 20 yr, stocking programs have supplemented natural walleye reproduction and have attempted to establish a self-sustaining channel catfish and muskellunge sport fishery (Enblom 1977).

There is no commercial fishery in the HW river or HW lakes. Although sport fishing is common along the river, it is concentrated in HW lakes, which are easily reached by all-weather roads, and from public launching ramps, summer homes, camp grounds and resorts. The lakes are fished heavily in summer, and to a lesser degree in winter, by angling and dark house spearing (the latter for northern pike and coregonids).

Physical characteristics of the 9 HW lakes are presented in Table 2. Even though hypolimnetic dissolved-oxygen levels routinely fall below 3.0 $mg \cdot L^{-1}$, all lakes deeper than 15 m contain cisco. Lake whitefish, usually indicators of oligotrophic conditions, are found in lakes Bemidji, Cass, Winnibigoshish, and Pokegama. Wind action often prevents thermal stratification of the largest lakes. Walleye, northern pike, and muskellunge are the most sought-after fishes. Walleye harvest has increased over the years in most HW lakes, but average fish size has declined.

Typical sport fisheries for walleye, northern pike, yellow perch, rock bass, and muskellunge exist in lakes Cass, Andrusia, and Big Wolf (Strand 1980). The three lakes supported an average of 250 294 angler hours during the summers of 1971–75. Average harvests ($kg \cdot ha^{-1}$) in Lake Andrusia were walleye 0.53, northern pike 0.49, yellow perch 0.44, rock bass 0.07, and muskellunge etc. trace. Winter fishing pressure (mainly darkhouse spearing) was

6.4 %, 10.3 %, and 11.5 % of the mean annual summer fishing pressure (fisherman–hours) on Cass, Andrusia, and Big Wolf, respectively, in 1971–75. Average yearly spearing harvests ($kg \cdot ha^{-1}$) in Lake Andrusia were northern pike 0.18, lake whitefish 0.13, white sucker 0.06, and cisco 0.06.

Lakes Cass and Winnibigoshish have high walleye reproduction potential; a portion of the walleye eggs collected there are returned annually as fry, but many are stocked into lakes Irvin, Bemidji, Big Wolf, and Andrusia where walleye reproduction is minimal. Northern pike and muskellunge are often stocked into the HW lakes (Kucera and Peterson 1980).

Lakes Bemidji, Big Wolf, and Cass are becoming increasingly eutrophic; significant percentages of phosphorus and nitrogen loadings are attributable to known point sources (Kucera and Peterson 1980). Lake Bemidji suffers frequent coregonid summer kills due to insufficient dissolved oxygen in the hypolimnion (Minn. Dept. Nat. Resources unpubl. lake surv. rept. 1982).

Upper Mississippi River (UMR)

UMR habitats can be generalized into eight categories: tailwaters, navigation pool, river lake or pond, slough, main channel, main channel border, side channel, and mouth of tributary (Fig. 5). Important components of main channel border, side channel and navigation pool habitats are dike fields and littoral areas (Rasmussen 1979; Environ. Sci. and Eng. 1982).

Tailwaters, which extend 0.8 km downstream from each navigation dam are characterized by well-oxygenated waters due to epilemnetic discharge via roller gates; currents are strong and sediments are coarse. Tailwaters provide one of the river's richest sport fisheries for walleye, sauger, white bass, freshwater drum, and catfishes. Paddlefish and shovelnose sturgeon are also present. Gizzard shad, carp, freshwater drum, and white bass usually dominate catches based on electrofishing, trammel and gill netting, and trawling. Shannon-Weaver diversity indices averaged 2.35 (Environ. Sci. and Eng. 1982). Tailwater fish assemblages were comprised of 23.6 % game species, 39.9 % commercial species, and 36.5 % forage species (Dunham 1971). Waters (1976) reported a catch rate of 2.7 $fish \cdot hr^{-1}$ (mainly white bass) at L & D 16. In a predominantly channel catfish and freshwater drum fishery below L & D 24, Farabee (1980) reported catch rates of 0.23–0.45 $fish \cdot hr^{-1}$. Boland and Ackerman (1982) reported catch rates from October to April of 0.35 and 0.45 $fish \cdot h^{-1}$ for the walleye/sauger fisheries at L & D 10 and 12, respectively. The MR Work Unit (1980) reported catch rates of 0.43 in spring and 0.63 in fall for the predominantly walleye/sauger fisheries of Pools 7, 8, and 9. In a 15-yr study (1967–81) of continuous walleye/sauger fishing in Pool 4, Thorn (1984) found no adverse effect on the naturally reproducing populations. Total harvest was dependent on year-class strength, which was highly correlated with water levels during spawning and incubation.

Navigation pools, which extend upstream from dams to a point where natural (pre-impoundment) channel conditions become evident, are more lentic than lotic in character, relatively shallow, and heavily silted. Although they generally lack structure, limited cover and hard substrates are found among stumps, dead trees, wing dikes, and riprap. Vegetated littoral areas provide important spawning and nursery habitats (Holland et al. 1983b). Holland and Sylvester (1983) found fish larvae, especially freshwater drum and gizzard shad, to be abundant in the pools in June and July. Gizzard shad, freshwater drum, carp, shortnose gar, smallmouth buffalo, bluegill, and black crappie are the most abundant species (Environ. Sci. and Eng. 1982).

Floodplain lakes and ponds are lentic habitats, often isolated from the river except during high flows. Depending on physical and chemical features, particularly water depth, they may support a significant sport fishery for centrarchids and esocids. However, they are difficult to manage due to the lack of water-level control, oxygen depletion, and an abundance of rough fish species such as carp. Gizzard shad, carp, bluegill, largemouth bass, black and white crappie, buffalo, and white bass are abundant, but species composition varies widely among lakes and with river stage (Environ. Sci. and Eng. 1982). Those lakes that have relatively deep water and are not highly eutrophic have diverse sport fish communities, while those that are very eutrophic and shallow are dominated by commercial and forage species.

Sloughs are lakelike habitats that maintain connections to the main river but do not receive fresh river flows except during high stage. They are much warmer than the main channel and may stratify thermally. They offer excellent spawning and rearing habitats for many species, including carp, esocids, centrarchids, and ictalurids. Fluctuations of water level in these shallow habitats can be critical to the spawning success of fishes that utilize inundated terrestrial vegetation, sand, or snags. Sloughs provide excellent seasonal sport and commercial fisheries. Standing stock estimates (Pitlo 1987) range from 43.8–931.5 $kg \cdot ha^{-1}$ in UMR-2, 44.0–724.2 $kg \cdot ha^{-1}$ in UMR-3, 437.8–778.5 $kg \cdot ha^{-1}$ in UMR-4. Dominant species include gizzard shad, shortnose gar, carp, bluegill, smallmouth buffalo, and freshwater drum (Environ. Sci. and Eng. 1982).

Main channel habitat includes the maintained navigation channel (minimum width 122 m, minimum depth 2.7 m) and is characterized by swift currents, sand or gravel substrates, and deep water. Disturbance by barge traffic and lack of structure limit the fishery in the main channel; however, it is an important habitat in UMR 1–4 where catfish use it as prime wintering (Hawkinson and Grunwald 1979; Talbot 1982) and nursery habitat (Helms 1975; LGL Ecol. Res. Assoc. 1981). Collections include channel catfish, silver chub, mooneye, flathead catfish, shovelnose sturgeon, and freshwater drum.

The main channel border extends from the navigation buoy line to the shoreline. Substrates include silt, sand, submerged and emergent wing dikes, and riprap. Standing crop is variable depending on season and river stage. Standing stock estimates (primacord samples; primarily carp, buffalo, catfish, white bass, and freshwater drum) varied from 0 to 3 016.8 $kg \cdot ha^{-1}$ (Rasmussen et al. 1985). The unusually large estimate was made during low stage, when schools of shovelnose sturgeon, smallmouth buffalo, freshwater drum, and channel catfish had retreated to a deep trough on the main channel border from other habitats. Of the 83 fish species reported from Pool 5A (Van Vooren 1983), 58 were collected during surveys of main channel border habitats (Ecol. Analysts 1984; Anderson et al.

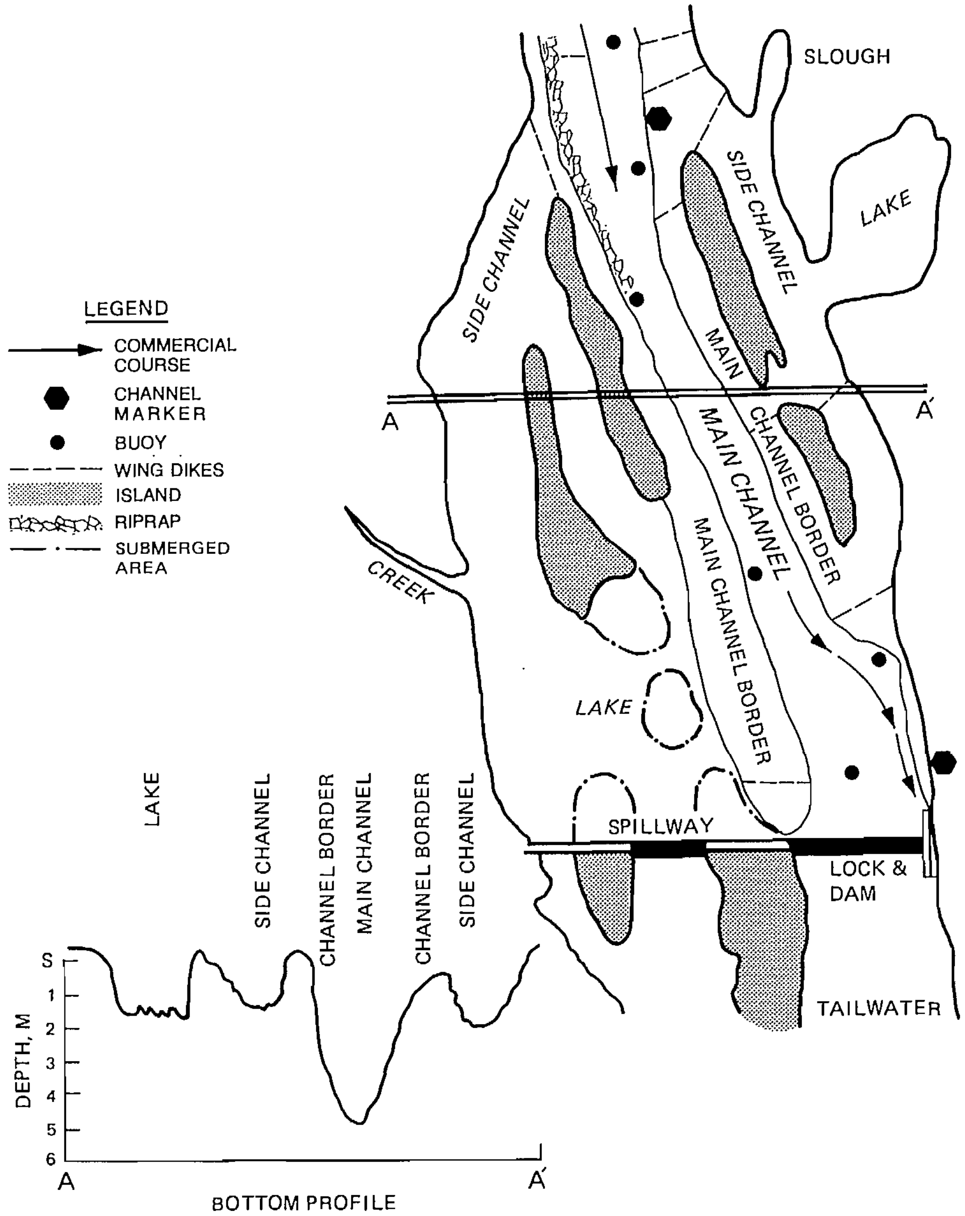


FIG. 5. Hypothetical section of Upper or Middle Mississippi River displaying habitat classification scheme developed by Upper Mississippi River Conservation Committee (Rasmussen 1979).

1983). Submerged dikes and riprap, typical of the main channel border, enhance habitat diversity and may support lush benthic communities (Hall 1980).

Dike fields, defined as areas encompassing three or more dikes, are an important component of main channel border habitat. Depending on location (side channel closure, inside or outside bend), construction (pile or stone, emergent or submergent), and design (L- or T-shape, notched or unnotched) they can provide excellent habitat where rock substrate is scarce. Submergent rock or pile dikes near the thalweg on outside river bends provide optimum habitat (Pitlo 1985). Dike fields are concentation areas for walleye, sauger, channel catfish, smallmouth bass, white bass, black crappie, bluegill, redhorse, freshwater drum, and smallmouth buffalo (Pierce 1980; Holzer 1980; Pitlo 1981). Pitlo (1985) reported average catch rates of 1.3–1.8 fish•hr^{-1} from wing dikes and closing dams in Pools 10, 11, 13, 16, and 18; predominant were freshwater drum, bluegill, catfish, and walleye. Notching of emergent dikes in the Missouri River has been beneficial to fisheries by enhancing habitat diversity (Robinson 1980). The St. Louis Corps of Engineers District is currently cooperating with fish and wildlife agencies to evaluate a similar program on the MR (Strauser 1987).

UMR littoral areas are important components of main channel borders, side channels, and navigation pools; they are of sufficient biotic value to merit distinction as an additional habitat type (Environ. Sci. and Eng. 1982). They contain macrophyte beds and usually extend outward about 8 m from the shore, but they can be more extensive if associated with submerged islands and stump fields, depending on depth, water clarity, and protection from wind. Littoral habitats provide nursery areas for many fish species and sport fisheries, primarily for centrarchids. Holland and

Huston (1983) stressed the importance of aquatic vegetation for larvae of UMR fishes.

Side channels generally flow behind islands and dredged material deposits and carry flow during most of the year. Many are partially blocked by stone dikes or closing dams but are used by commercial and sport fish. Standing stock estimates range from 79.1 kg•ha^{-1} in UMR-5 to 152 kg•ha^{-1} in UMR-2 (Pitlo 1987).

Tributary mouth habitat extends into the MR and up the tributary a distance equal to the width of the tributary (Environ. Sci. and Eng. 1982). It serves as staging, spawning, and feeding area for walleye, sauger, white bass, and paddlefish. Tributary mouths offer seasonal sport and commercial fisheries because many species congregate there prior to spring tributary spawning runs.

Middle and Lower Mississippi River (MMR and LMR)

MMR and LMR aquatic habitats may be categorized by their location on the floodplain or between the channel banks (Fig. 6). Floodplain habitats consist of lakes of various geomorphic origin, tributary channels, and such man-made waterbodies as levee borrow pits, water treatment lagoons, harbors, and canals (Cobb and Clark 1981). Floodplain lakes are much more numerous on the LMR than on the MMR; the largest and most common are oxbow and abandoned channel lakes formed by meander loop neck cutoffs and pointbar cutoffs. Scour channel lakes that occupy swales are also abundant but generally small. Other lake types are batture lakes (Gagliano and Howard 1984), floodplain depression lakes, and crevasse lakes. Ryckman et al. (1975) reported 242 lakes >0.08 km^2 in surface area on the LMR leveed floodplain; their total surface area at low flow was 425 km^2, including 181 km^2 of levee borrow pits. Ten oxbow lakes exceeded 4 km^2. Large areas inundated by flood flows provide additional ecologically important habitat.

The highest densities of larval fishes in the LMR occur in backwaters where the ichthyoplankton community is of a distinctly different composition than that of the river proper (Beckett and Pennington 1986). Backwaters are also important nurseries for juvenile fishes. Rivers such as the Ohio have large backwater areas which are created as tributary streams enter the river. The LMR, by contrast, has few tributaries.

Protection of backwaters is imperative on the LMR because they are ecologically very important and are in relatively short supply. Dikes and revetments prevent channel meandering, and new abandoned channels are rarely created (Nunnaly and Beverly 1984). Furthermore, the ultimate fate of all LMR abandoned channels is to fill with sediment (Gagliano and Howard 1984).

Aquatic macrohabitats of the channel environment include the main river channel, secondary channels, sandbars, gyres aggrating below bars, tributary mouths, natural banks, and areas associated with dike systems and revetted banks (Cobb and Clark 1981). These habitats are lotic in character except at very low stages when slack-water conditions may be found in some dike systems (Cobb and Magoun 1985) and secondary channels (Cobb and Clark 1981). During low flow, Ryckman et al. (1975) found 1 375 km^2 of water surface area in the LMR channel environment, including 1 061 km^2 of the main channel >1.5 m deep, 158 km^2 of the channel <1.5 m deep, 68 km^2 of chutes, and 88 km^2 of slack-water areas.

LMR aquatic habitats are characterized by pronounced annual variations in surface area, volume, depth, and relative spatial distribution associated with changes in river stage. Cobb and Clark (1981) found that the total surface area of aquatic habitat for an 80-km reach exhibited a threefold increase as river stage rose 7.7 m. Ratio of total channel to total floodplain surface area changed from 2.3 (stage = 4.0 m), to 3.3 (stage = 7.5 m), to 1.2 for overbank flow condition (stage = 11.7 m). Spatially, main channel was the predominant habitat type at low flow; main channel and sandbars were predominant at medium flow; sandbars and inundated floodplain were predominate at overbank flow condition.

The swiftly moving waters of the LMR provide ample habitat for such rheophilic fishes as shovelnose sturgeon, blue sucker, and blue catfish (Fig. 7). High energy systems

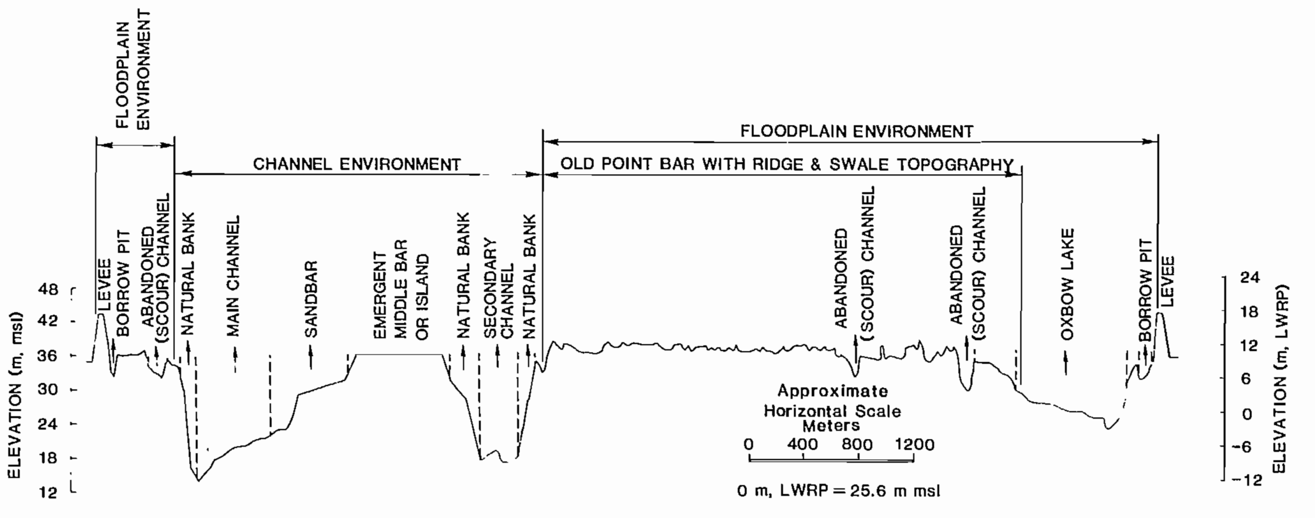


FIG. 6. Topographic cross section of the leveed floodplain and channel of the Lower Mississippi River (RKM 846 AHP) depicting locations and boundaries of geomorphically defined aquatic habitat types (Cobb 1988).

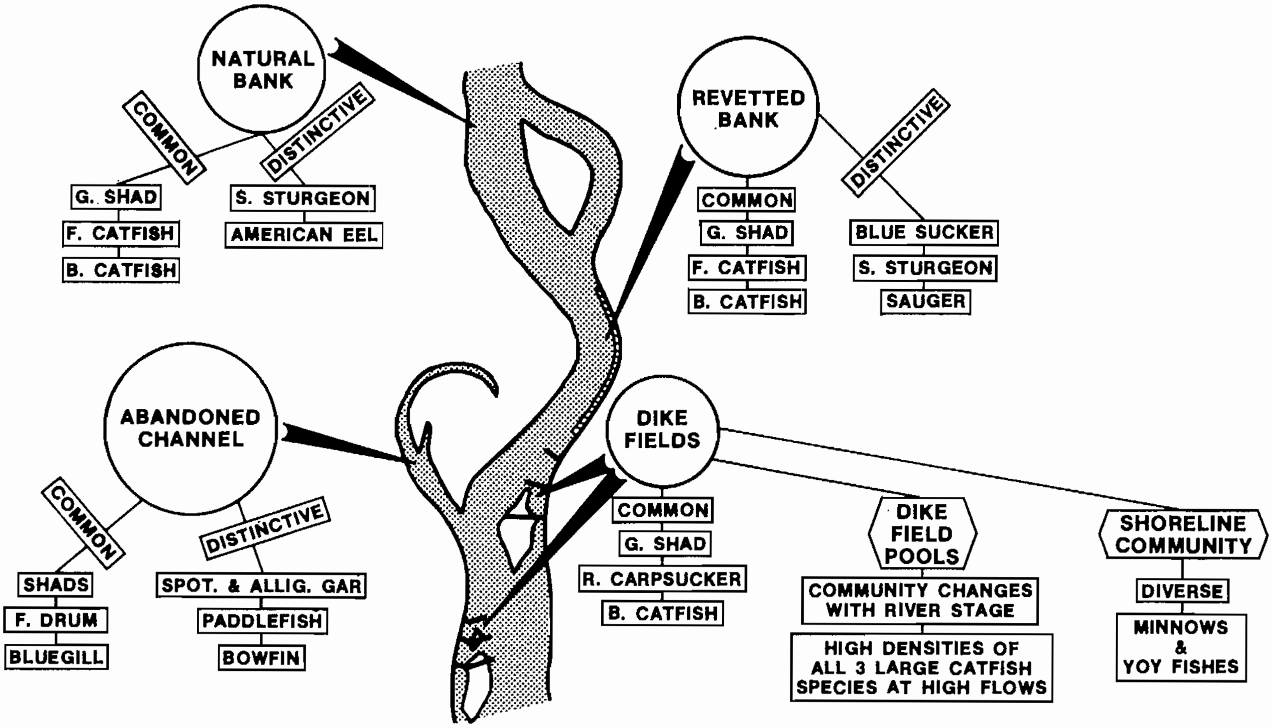


FIG. 7. Schematic drawing of Lower Mississippi River fish composition showing both the most common and distinctive species for the investigated habitats. Some characteristics of dike field fish communities are also shown. From Beckett and Pennington (1986), used with permission of the authors.

have been favored by USACE channelization practices (levees, cutoffs, revetments, and dikes). Lentic environments are important, therefore, because they provide habitat diversity for a variety of species. Those that are restricted to backwaters include black, brown, and yellow bullhead, bowfin, spotted gar, and young threadfin shad. Other species such as bluegill, largemouth bass, white and black crappie, paddlefish, and alligator gar show a marked preference for backwater areas (Pennington et al. 1980, 1983; Cobb et al. 1984; Beckett and Pennington 1986). The average standing stock of 666 kg•ha^{-1} in borrow pits along the LMR (Cobb et al. 1984) is consistent with standing stock estimates made in similar habitats in Louisiana, Mississippi (Lambou 1959; Bingham 1969; Bryan and Sabins 1978) and the UMR (Pitlo 1987). One rotenone sample in the Kaskaskia side channel of the MMR (RKM 1 723) produced 35 fish species with a standing stock of 1 035 kg•ha^{-1}, mainly gizzard shad, carp, and bigmouth buffalo (Environ. Sci. and Eng. 1982). This finding emphasizes the importance of side channels to the unpooled river as nursery areas and as refugia from the swift currents and harsh environments of the thalweg.

The physical, chemical, and biologial features of dike fields along the LMR are intermediate between those of channel and floodplain habitats. Dike fields often support the most diverse fish populations (Pennington et al. 1983) and a diverse ichthyoplankton community (Beckett and Pennington 1986) because of their physical structure (middle bars and the dikes themselves) and because of the varying physical conditions within dike fields as river stage changes. In most LMR dike fields, extensive sand and gravel middle bars occur between succeeding dikes and below the last dike. During high-river stage, the bars and dikes are submerged and current velocities approximate those of the main channel. During low flow, however, extensive pools are formed between the dikes, the river bank, and the middle bars. LMR dike fields, because of their biotic diversity and their depositional substrates at low river stages, are important habitats. However, their beneficial effects are lost if, as in the case of the Missouri River, they accrete sand until they become terrestrial (Beckett and Pennington 1986). Sedimentation is an important phenomenon, but filling rates and conditions leading to the establishment of dynamic equilibrium have not been determined. Some LMR dike fields, as presently constructed, have limited life expectancies as aquatic habitats. Typically, they accrete sediment, their middle bars are colonized by willows and cottonwoods, and they fill in. Engineering designs that would maintain and extend their aquatic life would be ecologically beneficial.

Non-revetted river banks are usually steep and are typically composed of silts and clays interspersed with sand layers. They are characteristically honeycombed by burrowing mayflies (*Tortopus incertus* and *Pentagenia vittigera*) (Beckett et al. 1983). Fallen trees and snags provide substrate for macroinvertebrates. Revetted banks are armored with stone riprap, articulated concrete mattress, or asphalt. Isolated areas of sediment may overlay the revetment. Current speeds on revetted banks are usually high, commonly exceeding 1 m•s^{-1}.

Atchafalaya River (AR)

AR habitats are more diverse than those of LMR because of comparatively limited AR channel modifications, remoteness of levees from the mainstem AR, and the braided channel on the lower 135 km of the AR course. These habitats are contained within a small geographic area and upon inundation by nutrient-rich river water, create a large nursery area per linear km of river during most water years (Bryan and Sabins 1978). Thus, a large number (approximately 0.7) of fish species occur per linear km of river (Table 4).

Fisk (1952) described morphologic and hydrologic changes accompanying the transition of the AR Basin from a lacustrine to a wetland environment before and after input from the LMR. At present, virtually the entire range of current speeds (from fast to nil), substrates (from gravel or coarse sand to compact clay or muck), and water quality (from high filterable residues to clear humate-rich water, to lakes with dense phytoplankton) can be found within a short distance from the main stem. Each habitat has a characteristic flora and fauna during low summer and fall water stages, but there is considerable overlap in species distribution among habitats, depending on river stage, season, and type of community.

Habitat types described by Bryan et al. (1977), grading from lotic to lentic within the AR, were: (1) mainstem river or distributary, (2) open-end canal, (3) headwater lake, (4) dead-end canal, (5) bayou, (6) backwater lake, and (7) swamp. Each habitat was evaluated using standing stock, relative abundance, frequency of occurrence, and diversity of species data gathered twice-monthly during a 4–yr investigation of phytoplankton (Sager and Bryan 1980), microzooplankton (Holland et al. 1983a), crustacean zooplankton (Binford 1975), benthos (Beck 1977), and fishes (Bryan and Sabins 1978) of the unleveed and leveed AR. Headwater lakes, open-end canals, backwater lakes, and bayous, respectively, were rated the four most important habitats in terms of abundance and diversity of biota (Bryan et al. 1977).

The average fish standing stock estimated from the lower (unleveed) AR was 860 $kg \cdot ha^{-1}$, which was 55 % higher than the upper (leveed) AR estimate of 550 $kg \cdot ha^{-1}$ (Bryan and Sabins 1978) and higher than other estimates made in Louisiana (Lambou 1959; Lantz 1974) and in virtually all southeastern reservoirs (Leidy and Jenkins 1977). Over 50 % of the catch in the Upper AR was gizzard shad, while yield of sport (centrarchids) and commercial (ictalurids) species was 8–10 times larger in lower (unleveed) AR habitats. Standing stock estimates made in the lower AR habitats were nearly 15 % greater following high-water years than low-water years. In low-water years, the yield of commercial species was halved while the proportion of forage species (gizzard shad and mullet) increased fivefold. Bryan and Sabins (1978) hypothesized that during low-water years primary production was relatively high and allochthonous input relatively low, thus encouraging production of such primary consumers as clupeids, mugilids, and cyprinids.

Succession (i.e., alteration or filling) is rapidly proceeding in riverine-distributary, open-end canal, headwater lake, dead-end canal, backwater lake, bayou, and swamp habitats, approximating the degree and order of flushing with increasing AR stages. Stagnation (with concurrent water-quality problems) in lentic habitats (i.e., swamp and bayous) primarily stems from accrual of allochthonous material and water hyacinth (Bryan and Sabins 1978; Holland et al. 1983b). The high diversity and production of flora and fauna in the AR appears to result from regular flooding and dewatering of habitats. However, because of the great sediment load of the AR main stem, productive habitats (lakes, canals, and bayous) are rapidly filling or being cut off from mainstem influence by delta building and accrual of allochthonous materials.

Investigations of MR ichthyoplankton distribution have shown the importance of backwaters and floodplain habitats to early life stages (Gallagher and Conner 1980; Schramm and Pennington 1981; Boyer 1978; Conner et al. 1983; Holland and Sylvester 1983; Holland et al. 1983b; Holland 1986; Clary 1985; Clary and Bryan 1985). The backwater ichthyoplankton community has a distinctly different composition than that of the river proper; the highest densities of larval fishes in the river system occur in floodplain lakes (Boyer 1978; Clary and Bryan 1985).

Energy Flow

The energetics of MR ecosystems have not been defined in detail. No data are available from the HW and MMR, and only one investigation has been conducted on the LMR, but detailed studies have been conducted in UMR Pool 19.

The largest carbon inputs and outputs in Pool 19 are via main channel river flows (Table 5), and most carbon is transported during major spring floods and irregularly occurring fall floods (Fig. 8). The latter probably result from the combination of reduced evapotranspiration due to leaf senescence and lower temperatures, a slight increase in rainfall, and increased runoff attributable to removal of substantial crop cover by harvesting. During the ascending limb of the spring flood, most carbon input is particulate (POC) (1.2 μm – 1.0 mm), but dissolved carbon (DOC) (less than 1.2 μm) is the dominant fraction during the remainder of the year. POC presumably washes in from floodplains and aquatic plant beds during the spring rise. Downstream DOC output is usually greater than POC output indicating that some of the POC inputs are utilized, stored, or converted to DOC within the pool in the spring. Total organic carbon (TOC) from municipal and industrial sewage comprises only 0.04 % of total inputs, much less than the load delivered by tributaries or from the unleveed floodplain (Table 5).

Aquatic macrophyte production in Pool 19 is approximately 8 times that of phytoplankton, excluding summer production in floodplain lakes, and the floodplain contribution of carbon to the water is approximately 5 times greater than the aquatic macrophyte production (Table 5). However, phytoplankton may contribute more autochthonous carbon in other river reaches. In the LMR, Sabol et al. (1984) estimated that phytoplankton biomass made up 20 % of the total particulate organic matter (POM) in the main channel and an abandoned channel lake near Greenville, Mississippi (RKM 821). Peak algal biomass in an abandoned river channel (backwater) near Greenville (9 600 $mg \cdot m^{-3}$ ash-free dry weight), calculated from chlorophyll *a* concentration, exceeded peak biomass of 210 $mg \cdot m^{-3}$ in Pool 19 (Engman 1984).

Pool 19 continues to accumulate sediment 73 yr after the dam was closed, and 300–700 g $C \cdot m^{-2} \cdot yr^{-1}$ is buried in off-channel areas where sediments accumulate — approximately 5 % of the total input (Table 5). Invertebrate and microbial respiration accounts for 11.6 % of the inputs,

TABLE 5. Annual carbon inputs, burial, utilization, and downstream loss for Pool 19, Mississippi River.

Inputs	kg Carbon × 10^6	% of Total Input
Upstream[a]	1 141	85.73
Tributaries[a]	90	6.76
Floodplain[b]	81	6.09
Sewage, Industry[c]	0.54	0.04
Aquatic macrophytes[d]	16	1.20
Phytoplankton[e]	2	0.15
Total Inputs	1 331	100.00
Burial, Use, Loss		% of Total Input
Burial[f]	73	5.48
Respiration[g]	154	11.57
Duck consumption[h]	0.15	0.01
Fish harvest[i]	0.04	0.003
Downstream[a]	1 322	99.32
Total Burial, Use, Loss	1 549	116.39

[a] Based on depth-integrated TOC samples taken on transects from 1982 to 1985 during stable low-flow periods (midsummer-fall) and during rising and falling stages of spring floods in 1983 and 1985. Tributaries were sampled at the farthest downstream point that was not subject to the backwater influence of the main river. Sample size (N) = 93 for the 2 largest tributaries, which accounted for 95% of all tributary input. Upstream inputs were measured at Lock and Dam 18 (LD 18), N = 87, and downstream outputs at LD 19, N = 149. No samples were taken below dams in Jan. and Feb., so in-pool concentrations of TOC were used.

[b] Differences between depth-integrated TOC samples on transects above and below Burlington Island, Nov. 1984–Oct. 1985, were extrapolated to entire floodplain (Grubaugh and Anderson 1988).

[c] Calculated from monthly 5-day BODs from sewage and industrial plants in 1982.

[d] Production per m^2 calculated from monthly standing crop and lear turnover of above-ground biomass for the dominant emergents *Sagittaria latifolia* and *Nelumbo lutea* (Grubaugh et al. 1986) and multiplied by total area of aquatic macrophytes.

[e] Product of carbon content, turnover (Harris and Piccinia 1977), cell volume (Tiffany and Britton 1971), seasonal algal cell counts (Engman 1984) and total pool volume.

[f] Based on an average organic C content of sediments in depositional areas of 2.1% by weight (Cahill and Autrey 1987; Cahill et al. 1987) and average annual sediment deposition determined from dated sediment cores (Cahill and Autrey 1987) and a sediment sediment budget (Bhowmilk and Adams 1986).

[g] Assumed carbon respired was 3× carbon incorporated in biomass of invertebrates (R. V. Anderson, Biological Sciences Dept., Western Illinois University, Macomb, IL 61455, unpubl. data) and bacteria (Henebry and Gorden 1988).

[h] Estimated consumption of fingernail clams by diving ducks (Thompson 1969, 1973).

[i] Based on average sport fish harvest in Upper Mississippi River of 8.9 kg•ha^{-1} and on reported commercial harvest of 331 115 kg (annual average 1973–77) in Pool 19 (Rasmussen 1979). Assumed carbon content of fish = 0.10 of wet weights.

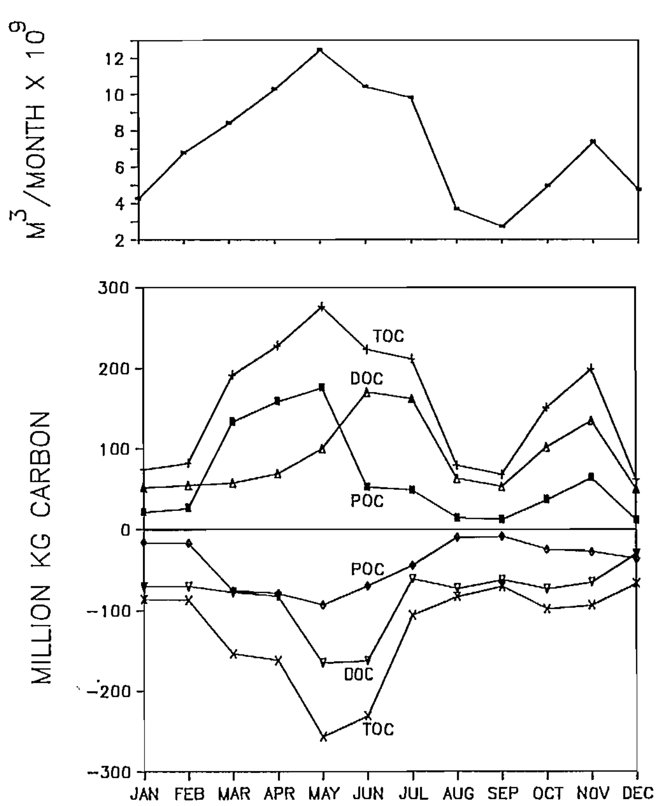


FIG. 8. Monthly discharge (top) and estimated monthly carbon fluxes (bottom) for 1984, Pool 19 UMR. Values below 0 are sums of downstream losses, burial, and respiration (see Table 5). TOC = total organic carbon, DOC = dissolved organic carbon, POC = particulate organic carbon.

seemingly more than could be supplied by aquatic macrophytes and phytoplankton. The primary production estimate needs to be refined, however. The estimate in Table 5 is based on above-ground production for 2 emergent species, rather than on the net above-and below-ground production of the entire complex of submergent and emergent macrophytes and periphyton that occur in Pool 19. Plant respiration was not estimated. Up to half the benthic respiration in some channel borders is attributable to macroinvertebrates (Butts et al. 1982), including fingernail clams which reach maximum standing crops of 97.3 g•m^{-2} (dry weight, excluding shells) (Gale 1969). Diving ducks and most commercially important fish species consume benthic macroinvertebrates (Ranthum 1969; Jude 1968, 1973). In terms of fish production, the main carbon pathway appears to be from detritus to benthic macroinvertebrates to fish.

Although TOC contributions from floodplains and beds of aquatic vegetation are quantitatively smaller than main channel flows, they may be important in terms of nutrient quality. Dense benthic macroinvertebrate populations usually occur offshore from UMR aquatic macrophyte beds, suggesting that these plants furnish high quality detritus delivered offshore by secondary currents, winds, or wave wash from barge traffic (Anderson and Day 1986; Adams 1986). Marshes, beds of submergent aquatic vegetation, and backwaters were not considered by Risotto and Turner (1985) in their attempts to explain annual variations in commercial fish yield from the MR basin. Size of floodplain (as indicated by acreage of bottomland hardwoods) was one of three variables in their regression model that explained 55% of the variation in average commercial fish catch among states utilizing the MR. The floodplain is a potential source of organic matter for detritivorous fish and for the invertebrates that other fish feed upon, as well as a fish spawning and nursery area.

Sabol et al. (1984) found that concentrations of POM in the LMR fluctuated monthly near Greenville with a peak during the spring flood. Detritus accounted for an average of 80 % by weight of total POM in the main channel; high concentrations of detritus were also found in a secondary channel, a dike field, and an abandoned channel lake during flowing water. In the off-channel environments during August low flow, however, phytoplankton made up over half the total POM. Zooplankton made up less than 1.8 % of POM (0.18 $mg \cdot L^{-1}$) at all river stages in the main channel. In other habitats, the maximum mean was 3.4 % (0.31 $mg \cdot L^{-1}$). Concentrations of dissolved organic matter for flowing water periods were 6 to 7 times POM levels.

In summary, the amount of OC coursing through the MR appears to be far in excess of that required for biological productions, making the river a net exporter of OC to the sea. However, much remains to be learned about the quantity and nutritional quality of OC originating from various sources. OC from upland sources may consist largely of dissolved humic acids or refractory particles by the time it is delivered to the main stem by tributaries, the more nutritious fractions having been utilized or retained by upstream communities. High fish production probably requires a local source of primary production in the form of phytoplankton, aquatic macrophytes, periphyton, or floodplain vegetation, although the connection may be indirect, via the detritus pathway.

Water flow patterns certainly influence fluxes of OM, but the processes have not been well defined. Floods transport OM from production centers, facilitate movements of organisms to sources of food, and enhance or retard production of OM by scouring, mixing, leaching of nutrients, and altering light penetration. In the LMR and AR, inundated floodplains constitute 27 % or more of total water surface area and are important fish spawning and nursery areas. Young fish feed upon the plankton which develops in the expanded aquatic habitat, fertilized by nutrients released from the newly flooded soil. During both high and low flows, eddies along the banks may be important areas of concentration or production of organic matter (Adams 1986; Zimpfer et al. 1986).

Commercial Fish Harvest

The mainstem MR had commercial landings totalling 5 126 t with an exvessel value of $1,942,000 in 1975, about 19 % of the commercial landings in the total drainage basin. Four groups of fish accounted for 92.4 % of the landings: buffalo (21.1 %), carp (42.2 %), catfishes (16.5 %), and freshwater drum (12.6 %) (U.S. Dept. Commerce 1978). The value of processed (fresh, frozen, canned, and cured) products was estimated at $5,000,000 in 1975. Based on the estimated total water surface area of the MR (255 370 ha) at lowflow, the harvest in 1975 averaged 22 $kg \cdot ha^{-1}$.

Risotto and Turner (1985) concluded that fisheries of the MR basin as a whole are being exploited at nearly the optimal level (about 11 000–12 000 fishermen). Their conclusion was based on the observation that catch per fisherman declined and yields remained stable during the 1950s and 1970s, when fishing effort increased substantially. However, numbers of fishermen on the MR cannot be equated with numbers of licenses in determining catch per unit effort. In most states, one fisherman may purchase several licenses (e.g., one $10 license for 10 hoop nets, another for 100 ft. of webbing, etc.). On the UMR and MMR, commercial catch data in five states are turned in on a volunteer basis by fishermen to their respective conservation departments; the data are then compiled by the UMRCC. Because of taxes, catches may be under-reported. The number of licensed commercial fishermen in the UMR has remained relatively constant since 1984 at approximately 2 100 individuals, a finding that suggests traditional fishing territories and limited entry (Kline and Golden 1979a; UMRCC 1953–1982).

A slight upward trend in the reported harvest from the UMR occurred from 1953 to 1977 (Table 6), and that data may reflect increases in the stocks, increases in fishing effort, or increased efficiency of fishermen. Stocks might have increased commensurately with food supplies resulting from natural succession in the impoundments completed in the 1930s. As sedimentation occurred, the bottom was raised into the euphotic zone, and marshes and submerged macrophytes developed in many pools. They, in turn, could furnish detritus for the benthic macroinvertebrates, which are the preferred food for most commercial species. The introduction of light, durable nylon gill and trammel nets in the 1950s may have increased the efficiency of fishermen. Although an increase in the real value of freshwater fish might also stimulate increased fishing effort, evidence from Illinois indicates that wholesale prices (adjusted for inflation) have remained about the same since 1920 (Sparks 1984).

Commercial catch in the UMR was directly related to total surface area of water in the navigation pools $R = 0.90$ (Kline and Golden 1979a), $R = 0.91$, $P < 0.01$ (Lubinski et al. 1981). When this relationship was expressed as catch per unit area (CPUA), catches in Pools 8 and 18 were exceptionally high (Fig. 9).

Other factors that influence CPUA are suggested by comparing the catch in the UMR with the catch in one of its major tributaries, the Illinois River (Table 7). The highest values of CPUA in the Illinois River in 1980 were from reaches with the largest proportion of backwaters and lakes connected to the river (Richardson 1921). Many of these areas were drained in the 1920s, and CPUA declined; nevertheless it was still greater there in the 1950s than in the Mississippi. The Illinois River CPUA data are from a 362-km reach where the river occupies a large broad valley carved by the ancient Mississippi. The combination of low slope (2 $cm \cdot km^{-1}$) and oversize floodplain give the comparatively small Illinois the protracted flooding characteristics of a much larger floodplain river. The drastic decline in CPUA between the 1950s and the 1970s in the Illinois are attributable to filling of the remaining backwaters and lakes with sediment and toxic pollutants that decimated the benthic macroinvertebrates on which commercial species of fish feed (Sparks 1984). Navigation dams on the UMR initially increased the non-channel aquatic habitats and lowered the low flow-slope in the downstream ends of the pools, thereby making the UMR more like the Illinois of yesterday and probably increasing CPUA. Some UMR reaches have already returned to their pre-dam habitat proportions (Olson and Meyer 1976a, b); in others such as Pool 19, beds of aquatic plants and marshes are rapidly encroaching upon open-water habitat.

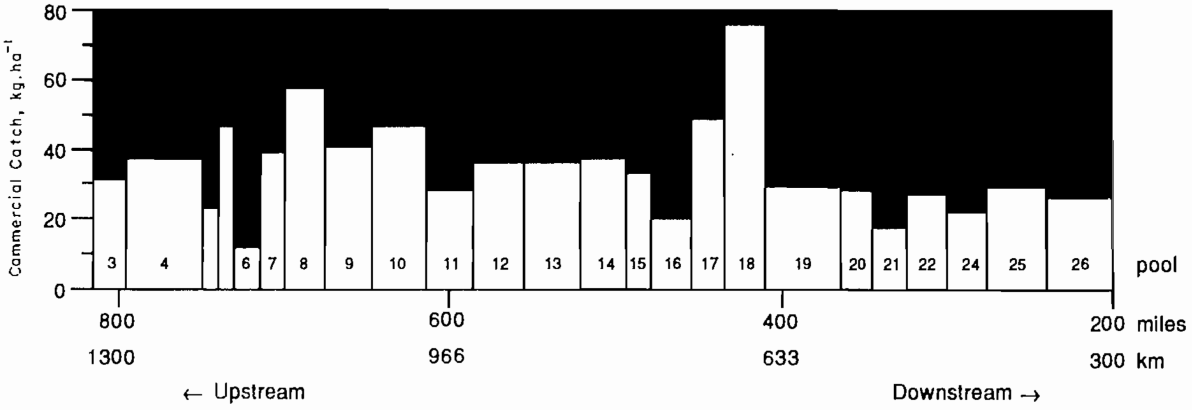
Commercial harvest data for the LMR and AR are

TABLE 6. Average annual commercial fish harvest (kg) and average number of licensed commercial fishermen reported at 5-yr intervals from UMR Pools 3-26 and the MMR between 1953 and 1982 (Kline and Golden 1979a, UMRCC 1953-1982).

	1953-57	1958-62	1963-67	1968-72	1973-77	1978-82
Carp	1 632 510	2 364 429	2 700 388	2 704 911	2 477 444	1 630 729
Buffalo	831 955	1 165 021	1 118 134	1 262 889	1 101 415	1 123 775
Catfish	731 435	845 335	770 389	649 860	661 090	635 510
Freshwater drum	475 333	568 224	646 381	769 923	655 542	577 827
Minor species[a]	239 880	200 151	198 809	231 679	269 892	271 841
Total harvest	3 911 113	5 143 160	5 434 101	5 619 262	5 165 383	4 239 682
Avg. no. fishermen	2 048	2 411	1 812	2 123	2 470	2 002
Avg. catch	1 910	2 245	2 999	2 647	2 091	2 118
Harvest[b] (kg•ha^{-1}	22.9	30.1	31.8	32.8	30.2	24.8

[a] Minor species include bullhead, carpsucker, sucker-redhorse, sturgeon, paddlefish, gar, bowfin, American eel, northern pike, crappie, yellow perch, mooneye, and goldeye.

[b] based on 1976 estimated 171,063-ha water surface area between Hastings, MN and Ohio River/Mississippi River confluence (Rasmussen 1979).



(Source: Lubinski, Wallendorf, and Reese, 1981)

FIG. 9. Commercial catch, CPUA (kg•ha^{-1}), in the navigation pools of the Upper Mississippi River. The x-axis refers to the distance upstream from the confluence of the Ohio and Mississippi, and the width of the bars indicates the length of the pools.

TABLE 7. Comparison of commercial catch per unit area in the Upper Mississippi and Illinois rivers.

Upper Mississippi River		Illinois River	
Year	kg•ha^{-1}	Year	kg•ha^{-1}
		1908	77.7 — 200.0[a]
1953-62	26.5[b]	1950-59	45.6[c]
1973-77	30.2[b]	1973-77	8.4[c]

Sources: (a) Richardson (1921); (b) Table 6 this paper; (c) Bellrose et al. (1977); Sparks et al. (1979); annual reports of fisheries statistics of the U.S. published by the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Washington, DC, 1950-77; water surface areas from Gilbertson and Kelly (1981).

difficult to assess and may be unreliable because of inconsistent methods of data gathering and reporting (Table 8). Records of Louisiana landings from 1966 through 1985 were furnished by the New Orleans District Office of the National Marine Fisheries Service (NMFS). However, data for 1961-65 were only available through the Washington, D.C. Offices of the U.S. Depts. of Interior and Commerce and do not include landings from coastal parishes. This accounts for the relatively small CPUA for the 1961-65 period. Each year from 1965 to 1977 (the last year when the statistics were published by drainage), CPUA reported by the District Office was 70-600% higher than that reported by the National Office. Also, the District Office relies on wholesalers to furnish the number of fishermen (pers. commun. L.T. Usie, Fishery Reporting Specialist, NMFS, New Orleans), who often combine catches from the LMR and AR, or more frequently, report their LMR catches from the AR to obtain best price because of locally reported taste and odor problems in LMR fish. The data are further confounded by the fact that up until 1978 commercial catches were assigned to waters within states. Thereafter Louisiana's landings were categorized either as freshwater

TABLE 8. Average annual commercial harvest (kg) of freshwater species for 5-yr intervals from 24 Louisiana parishes which border the Lower Mississippi River (RKM 0-797) and Atchafalaya River (RKM 0-507), 1961 through 1985.

	Year				
Species	1961–65[a]	1966–70	1971–75	1976–80	1981–85
Carp	7 757	9 600	99 983	109 519	82 941
Buffalo	228 223	219 804	657 162	1 540 305	1 060 961
Catfish	1 852 981	1 263 382	1 832 757	2 519 866	1 802 759
Freshwater drum	87 317	65 117	268 764	415 710	315 918
Crayfishes	385 064	592 266	2 305 186	2 928 143	2 683 736
Minor species[b]	2 657 849	8 544 958	4 619 217	1 680 562	630 903
Total harvest[c]	5 219 191	10 695 127	9 783 069	9 194 105	6 576 218
Total harvest[d]	1 696 237	2 724 162	3 934 778	4 540 418	—
Average number licenses sold					1 807
Catch/fishermen[c]					7 275
Harvest (kg•ha^{-1})[f]	24.4	50.1	45.8	43.1	30.8
Total Louisiana landings (freshwater and marine)					771 012 120

[a] Exclusive of landings from six coastal parishes.

[b] Includes gars, paddlefish, and bait fishes.

[c] Assumed 70 % of total Louisiana freshwater landings for Louisiana. (New Orleans data; see text).

[d] Data from Statistical Digests, Fishery Statistics of the U.S., Washington Office.

[c] Assumed an average of two licenses per fisherman (computed using total harvest[c]).

[c] Assumed a constant average surface area of 213 500 ha (computed using total harvest[c]).

or marine; thus, it is difficult to sort landings by drainage within the state. Since 1978, however, it is possible to determine the share of total Louisiana landings comprised by selected commercial species.

An average of 1 807 commercial fishing licenses were sold per year (1981–85) in the 24 parishes (including 6 coastal parishes) bordering the LMR and AR (Table 8). While the 24 parishes represent 38 % of Louisiana's 64 parishes, they account for only about 20 % of all licenses ($\bar{x} \doteq 11\ 500$) sold each year. To determine catch per fisherman, we assumed that each freshwater fisherman purchased an average of two licenses, and we estimated that 70 % of Louisiana's freshwater landings were made in the 24 parishes bordering the LMR and AR. Freshwater fishes and crayfishes comprised only 3 % of the value of Louisiana landings and only 0.8 % of the average annual total freshwater and marine Louisiana landings during 1981–85. Shrimp, menhaden, oysters, and other marine species obviously make up the major portion of Louisiana's fisheries products (NMFS, New Orleans), making it the leading state in fisheries landings.

Annual commercial harvests from the LMR and AR (1966–85) were highly variable because of changes in catch of clupeids and crayfishes, which varied by more than 300 and 800 %, respectively. Because many fish species are two years old and others as much as four years old before entering the harvest and because of such additional variables as differing cohort sizes and dominant year-classes within each species, total catch does not vary in any single, predictable way with discharge. Moreover, the diversified local economy, culture, and market (year-to-year and within year) leads to variation in commercial fishing pressure regardless of the availability of stocks. Total fish landings in LMR and AR increased annually through the 1960s, peaked at more than 13M kg in 1971, decreased markedly in the 1970s, and have fluctuated between 3 and 9M kg since 1979 (Table 8). Apparently because of a continued price rise, the buffalo and catfish fisheries steadily increased or held constant at least until 1980, in spite of vigorous growth in local fish culture. While there was a 28 % decline in total landings in 1981–85 compared with 1976–80, crayfish landings declined only 8 % (perhaps reflecting the $.08/lb average price increase).

Crayfish may be the best species to track to detect trends in LMR and AR commercial freshwater fisheries in relation to changes in habitat and water years. In the first place, the fishery is exploited; the price per pound has fluctuated inversely with the supply for the past 15 yr. Second, the majority of the catch and market are local; 95 % of the commercial crayfish fishermen work in the AR. Third, only two species, *Procambarus clarkii* and *P. acutus*, are valued commercially and their value to the market has equalled or exceeded that of all other species combined for the past 4 yr. Finally, the species provide an annual crop (few live more than one year), and their life histories are dependent upon overflow habitats. High water years yield high annual crops.

In the past 23 yr, annual value and total catch of crayfishes varied inversely on 19 occasions; the largest annual changes in crayfish crop value were associated with the greatest increases or decreases in total landings. Supply and demand phenomena are manifest each crayfish season. Prices are high in December or January when catches are low. If river stages have not inundated the swamp floor, or if water hyacinth nurseries have been frozen, catches may remain low and prices high throughout the spring. Without exception, total crayfish landings increased (and price decreased) with increased discharges, especially during warm, wet winters. During those years (e.g., 1973, 1975, and 1979) the entire AR swamp was inundated, and growth of terrestrial vegetation and water hyacinth (essential detrital forage base and nursery) was encouraged (Bryan and Sabins 1978).

The AR basin supports a significant sport fishery (Table

TABLE 9. Estimated annual sport fishing effort and harvest (kg) within the lower Atchafalaya River Basin, 1971 through 1974 (modified from Soileau et al. 1975).

	Year			Estimated yearly average
	1971–72	1972–73	1973–74	
Number interviewed	44 936	24 972	23 578	31 162
Sport fishermen	2 743	2 505	3 802	3 017
Effort (person-hours)				
Boat fishing	2 357	1 990	3 243	2 455
Bank fishing	386	515	558	482
Harvest				
Bass	571	262	702	488
Crappie	560	255	748	514
Other sunfish	1 566	960	1 917	1 429
Catfish	377	215	391	308
Other fish	149	46	130	107
Number of fish per hour	1.17	0.69	1.02	0.96
Crayfishes (kg × 10^3)	508	1 344	301	718
Crabs (dozens × 10^3)	13	28	14	18

9). Almost 33 % of 286 316 people leaving the lower basin via three major highways were interviewed (1971–74). Nearly 24 % had participated in some type of recreation, and about 45 % were sportfishermen. Among the sport fishermen, from four to six times as many hours were spent boat fishing as bank fishing. Yield to the boat fishermen was significantly higher, especially their catch of basses and crappies (Soileau et al. 1975). The significantly low CPUE, as well as the reduced effort in 1973, was due to a 100-yr flood that did not recede from the swamp floor until late July. However, there was a predictable two-to-five fold higher catch of crayfishes and crabs during that year compared with previous and subsequent years. This increase was predictable in view of the fact that a positive relation was established between area of AR floodplain inundated and yield of aquatic animals whose life spans approximate one year.

Fishery Assessment Problems and Techniques

Swift currents, large fluctuations in stage and discharge, deep water, wind-driven waves, floating debris, shifting substrates and navigation traffic are some of the obstacles to accurate assessment of MR and AR fishery stocks. Diversity of habitats and environmental conditions generally preclude the utilization of the same sampling gear in all habitats, thereby confounding catch comparisons. Similarly, the same gear cannot be used consistently in a particular habitat because environmental conditions change radically with river stage (e.g., changes from shallow, slack water to deep water and strong currents). Even the biology of fishes in large rivers may differ significantly from that in other habitats. UMR walleyes, for example, appear to be opportunistic, spawning successfully on rock as well as submerged vegetation (Holzer and Von Ruden 1984). Further, river bottom character and structure are difficult to describe efficiently and accurately because hydroacoustic techniques have not yet achieved the resolution necessary to operate effectively in shallow areas.

The MR is the political boundary for ten states. Consequently, management programs are often ignored because no state has sovereign rights to the resource, and dollars used to manage it are often viewed as wasted. The MR is considered dangerous by many because of swift currents, obstructions, and large commercial vessels. It also bears the stigma of being polluted because it receives industrial and domestic wastes.

To help overcome these problems, conservation agencies of Wisconsin, Minnesota, Iowa, Illinois, and Missouri formed the Upper Mississippi River Conservation Committee (UMRCC) in 1943. Located in Rock Island, Illinois, the UMRCC is coordinated by the U.S. Fish and Wildlife Service; its objectives are to promote the preservation and wise use of the natural and recreational resources of the UMR, and to formulate policies, plans and programs for conducting cooperative studies. The UMRCC provides biologists with a platform for organized action and a level of communication previously unattainable. There is no equivalent organization on the LMR.

The first UMR creel census (Pools 4–11) was conducted by the UMRCC in 1944–46 (Greenbank 1957). A more comprehensive UMRCC effort (summarized in Table 10) covering Pools 4, 5, 7, 11, 13, 18, and 26 at 5-yr intervals was initiated in 1962 (Nord 1964; Wright 1970; Fleener 1975). The census was expanded in 1976 to collect data on use of all aquatic and terrestrial resources (Fleener 1976). This latter technique, applied to a single pool, was adapted by the UMRCC to replace the 5-yr creel surveys. It has subsequently been used on Pools 5 and 9 (Watson and Hawkinson 1979; Ackelson 1979). Budget constraints and staffing commitments to major interagency long-term planning and development projects have prevented further cooperative UMRCC surveys; however, more are planned and numerous individual state creel surveys conducted on individual tailwaters and backwaters have been completed.

A variety of nets (Jackson et al. 1981) are used on the UMR: gill nets, trammel nets, seines, trawls (bottom and midwater), hoop nets, fyke nets, frame nets, and larval fish nets. In studies of main channel border habitats, Anderson et al. (1983) found bag seines and pulsed-DC electrofishing to be their most effective and unbiased gear when used at night.

For electrofishing, the UMRCC recommends pulsed DC

TABLE 10. Total estimated sport harvest for each species and each pool by number and weight (kg) from seven pools of the Upper Mississippi River during three identical UMRCC creel surveys (Kline and Golden 1979b).

Species		1962-63		1967-68		1972-73	
		Number	Weight	Number	Weight	Number	Weight
Lake sturgeon (*Acipenser fulvescens*)		47	320	0	0	0	0
Shovelnose sturgeon (*Scaphirhynchus platorynchus*)		199	81	22	25	359	218
Paddlefish (*Polyodon spathula*)		0	0	0	0	101	137
Gar (*Lepisosteus* spp.)		25	11	107	52	1 152	523
Bowfin (*Amia calva*)		168	99	417	450	255	369
American eel (*Anguilla rostrata*)		122	27	100	45	208	118
Gizzard shad (*Dorosoma cepedianum*)		52	4	0	0	1 859	843
Mooneye (*Hiodon tergisus*)		804	283	558	144	347	146
Northern pike (*Esox lucius*)		12 241	20 239	22 435	42 772	12 306	25 593
Carp (*Cyprinus carpio*)		11 203	12 535	17 185	25 574	16 467	16 765
Suckers (*Catostomidae*)		432	309	1 332	1 059	2 297	1 606
Blue catfish (*Ictalurus furcatus*)		1 008	198	5 118	1 882	1 184	240
Channel catfish (*Ictalurus punctatus*)		76 554	31 755	116 002	38 446	77 461	35 687
Flathead catfish (*Pylodictis olivaris*)		4 276	4 621	3 479	2 397	5 884	4 212
Bullhead (*Ictalurus* spp.)		25 742	8 754	29 112	5 107	14 720	3 983
White bass (*Morone chrysops*)		123 556	45 753	100 524	33 098	140 617	55 566
Yellow bass (*Morone mississippiensis*)		260	36	0	0	86	19
Rock bass (*Ambloplites rupestris*)		1 205	208	2 916	342	5 671	899
Warmouth (*Lepomis gulosus*)		72	10	2 019	212	45	5
Green sunfish (*Lepomis cyanellus*)		160	14	4 404	293	16 978	1 857
Orangespotted sunfish (*Lepomis humilis*)		76	5	0	0	0	0
Bluegill (*Lepomis macrochirus*)		537 587	76 483	414 280	60 331	350 510	51 099
Smallmouth bass (*Micropterus dolomieui*)		3 527	1 743	5 453	2 269	5 258	1 937
Largemouth bass (*Micropterus salmoides*)		24 961	18 134	37 804	23 600	19 970	12 352
Crappie (*Pomoxis* spp.)		397 322	79 779	366 469	85 240	219 445	54 930
Other sunfishes (*Centrarchidae*)		5 069	579	4 827	551	6 989	854
Yellow perch (*Perca flavescens*)		52 190	7 376	29 995	4 248	35 105	4 613
Sauger (*Stizostedion canadense*)		85 062	39 226	116 480	51 688	213 242	77 214
Walleye (*Stizostedion vitreum vitreum*)		34 116	31 514	77 347	59 783	92 811	59 436
Freshwater drum (*Aplodinotus grunniens*)		94 224	37 293	153 806	45 602	159 849	66 136
TOTAL		1 492 260	417 389	1 512 209	485 210	1 401 176	477 357
Pool	Harvest (kg•ha^{-1})						
4	15.86	340 304	135 560	377 925	175 672	312 071	137 474
5	13.58	195 620	55 746	134 081	59 529	168 937	77 655
7	13.04	444 943	94 562	258 634	75 701	327 493	75 727
11	9.58	191 259	54 126	290 458	64 830	329 446	112 315
13	3.44	123 646	20 965	228 121	53 946	160 399	42 629
18	5.83	105 024	41 217	140 437	37 951	14 852	4 022
26	2.85	91 464	15 213	82 553	17 581	87 978	27 535
TOTAL	—	1 492 260	417 389	1 512 290	485 210	1 401 176	477 357
AVG	9.17	—	—	—	—	—	—
Grand total estimated UMR harvest (Pools 1-26)		4 327 554	1 210 426	4 385 406	1 407 118	4 063 410	1 384 344
Estimated harvest (kg•ha^{-1}) for Pools 1-26		—	8.06	—	9.37	—	9.22
Avg. catch rate (All species fish•h^{-1})		0.869	—	0.884	—	0.901	—
Avg. fishing effort (h•ha^{-1})		31.1	—	34.7	—	30.5	—

units; however, some states continue to use AC units. AC units modified with deep water electrodes are used for sampling main channel wintering fish populations (Grunwald 1983). Efficiency of this gear is, however, limited since water clarity and buoyancy of stunned fish vary.

Rotenone is the primary toxic chemical used, but it is no longer used in flowing waters due to volume requirements and risk of kill outside the target area. Pitlo (1987) recorded only 25 instances of rotenone use in the UMR. Primacord was first used to make standing stock estimates in main channel border habitats of Pool 13 in 1983 (Rasmussen 1984; Rasmussen et al. 1985).

Fish tagging (jaw tags and Floy tags) has been used extensively on the UMR, at first to trace fish movements and more recently to estimate harvest. Fish tagging remains the method of choice for tracing movements of fish weighing less than 2 kg, but radio telemetry is now used extensively for larger fish. In the mid-1970s, externally attached transmitters were used (Fossum 1975; Bahr 1977). Radio transmitters have since been surgically implanted into the abdominal cavities of walleye, flathead catfish, sauger, buffalo, paddlefish, and largemouth bass (Holzer and Von Ruden 1984; Southall 1982; Talbot 1984; Pitlo 1985; Stang and Nickum 1985).

Extensive seasonal movements have been documented within and between UMR pools for paddlefish (Gengerke 1978; Southall 1982), walleye (Holzer and Von Ruden 1984), shovelnose sturgeon (Hurley and Nickum 1983), and white bass (Finke 1966a). Localized seasonal homing movements up and downstream to and from backwaters have been documented for flathead catfish (Talbot 1984) and northern pike (Finke 1966b). Van Vooren (1984) documented two cases of interpool movement of largemouth bass but noted that such movement was not common.

Hydroacoustic techniques have been adapted for use in the MR, but only limited data have been collected. While individual fish lengths and weights as well as population density can be estimated with this method, the technique is not usable in shallow (< 2-m) waters, is expensive, and does not permit identification of fishes. At present, the method appears best suited for defining spatial distribution patterns of total fish assemblages in large deep-water habitats, especially in the main channel. Sonar has been used to study rough fish movements under ice (Strand and Scidmore 1969), to document fish concentrations associated with bottom structure (MR Work Unit 1976, 1977), and to locate winter catfish concentrations (Larson and Ranthum 1977). Seagle et al. (1980) employed side-scanning sonar to assist in the characterization of Pool 26 habitat.

Wisconsin and Minnesota began successfully using SCUBA and photographic techniques in lieu of SONAR in the late 1970s to make observations of wintering condition of fish in Pool 4 main channel habitats (Hawkinson and Grunwald 1979; MR Work Unit 1979). Catfish become practically dormant during winter in UMR-1 through UMR-4, utilizing rocks and each other to provide shelter from the current (Hawkinson and Grunwald 1979; Talbot 1982; Lubinski 1984). Talbot (1984) estimated these concentrations at 49 834 channel catfish•ha^{-1} and 2 491 flathead catfish•ha^{-1}.

Fisheries Management

Introduction of Exotics

UMR fish stocking began in 1872 with unsuccessful introductions of American shad and Atlantic salmon (Carlander 1954). The first carp were caught in 1880 at Hannibal, Missouri; they were common as far north as Minneapolis by 1890. By 1899, commercial catch from the MR and its tributaries included 5.4M kg of carp (Townsend 1902). Coker (1930) attributed more than 44% (4.3M kg) of the 1922 U.S. commercial carp fishery to the MR. UMRCC records (Table 6) show estimated carp harvest in the UMR to vary from 1.6M kg for the period 1953–57, to a peak of 2.7M kg for 1968–72, with a return to 1.6M kg in 1978–82 despite little change in fishing effort. Kline and Golden (1979a) summarized commercial fish harvest (1953–78) and noted displacement of buffalo by carp as well as a decline in the carp fishery. Continued decline in carp harvest has been noted by the UMRCC Fish Technical Section. A portion of the reduced harvest has been attributed to U.S. Food and Drug Administration restrictions on the sale of fish contaminated with PCBs and heavy metals in Pools 3 and 4 (Kline and Golden 1979b). However, Lubinski et al. (1986) postulated that carp population declines and absent year-classes in the UMR may be related to poor recruitment during high or variable water years.

The grass carp first appeared in the UMR commercial fishery in 1975 when 257 kg were recorded for Pool 25 (Kline and Golden 1979a). Grass carp have since moved upstream to Pool 5A; reported harvest for the entire UMR in 1983 wat 6 051 kg (UMRCC 1985). Natural reproduction in the UMR has not been reported, but evidence of reproduction has been reported on the LMR (Conner et al. 1980) and on the AR, Red, Black and Oachita rivers (Zimpfer et al. 1987).

Introduction of striped bass and "wipers" (striped bass-white bass hybrids) has been controversial (Skrypek and Sternberg 1978; Ackerman et al. 1978) because of fear of direct competition with walleyes. Neither Minnesota nor Iowa has been successful with striped bass introductions. Wipers are currently being introduced and evaluated in Pool 14 (Stoeckel 1985).

Other exotics such as salmonids, rainbow smelt, and goldfish appear as strays in the MR fishery (Table 4), but none occur in significant numbers.

Fish Rescue

Fish rescue programs began in Iowa in 1876. Their purpose was to salvage fish stranded in backwaters by seasonally receding water levels. Similar programs, begun in 1889 by the U.S. Fish Commission peaked between 1917 and 1923 (Carlander 1954). Impoundment of the UMR in the 1930s stabilized water levels and ended fish rescue operations.

Refuges

The UMR Wildlife and Fish Refuge (UMRWFR) was established in 1924, the result of lobbying by the Isaak Walton League of America (IKES) for a refuge primarily for protection of smallmouth bass (Fairchild 1982). Today, the UMR contains three National Wildlife Refuges: UMRWFR — 78 975 ha (1924); Trempealeau National Wildlife Refuge — 4 415 ha (1943); and Mark Twain National Wildlife Refuge — 13 090 ha (1958). Their major emphasis is migratory waterfowl management rather than fish management as envisioned by the IKES. The MR is the only river in the United States that has been designated for two major federal purposes — commercial navigation and wildlife refuges. Conflicts between these two authorizations and project purposes peaked in the 1970s. The result was Public Law 99-662 (1986), which designated the UMR System as a nationally significant ecosystem and a nationally significant commercial navigation system, and authorized a major ($190-M, 10-yr) Environmental Management Program (EMP) for the UMR and selected navigable tributaries.

Three wildlife refuges are located along the LMR in the Head-of-Passes area: Delta National Wildlife Refuge (19 440 ha), Bohemia Wildlife Management Area (13 365 ha) and the Pass a Loutre Waterfowl Management Area (26 730 ha).

Regulation

Harvest regulation began between 1895 and 1925 (Carlander 1954) with the establishment of license fees for commercial and sport fishing in each state bordering the UMR. Regulations proliferated, and conflicts over regulations and boundaries led to the organization of the UMRCC in 1943. The UMRCC has tried to standardize UMR fishing, hunting and boating regulations. Today, reciprocity is the general rule and standardization is the goal.

Recently recommended regulation changes include a 30.5-cm length limit for UMR catfish taken commercially (Helms 1969) and a 38-cm length limit for largemouth bass in pools 16–19 (Van Vooren 1984). Some emotionally and politically based regulations remain. One of these concerns walleye fishing during the spawning season in the UMR between Minnesota and Wisconsin. Another recently resolved problem concerns the prohibition of boating in the prime sport fisheries of lock and dam tailwaters. The USACE imposed a 91.5 m closure for safety reasons in the early 1980s. Through negotiation and political compromise, this restriction was reduced to 45.8 m in return for state cooperation in enforcement.

Habitat Management

Prior to environmental legislation of the late 1960s (National Environmental Policy Act), only minor attempts were made to manage MR habitats. Public Law 697, passed in 1948 and known as the Anti-Drawdown Law, was probably the most significant habitat management completed during that period. It ordered the USACE to maintain UMR navigation pools "as though navigation was carried on throughout the year." In earlier years, pools were drawn down in winter to increase capacity for spring floods; the result was devastating losses to fish and wildlife populations (Greenbank 1946).

In the 1970s, growing public support for environmental protection and management led to lawsuits over operation, maintenance (dredging), and expansion of the 2.7-m navigation project. The lawsuits, in turn, led to major interagency studies (GREAT I, 1980; GREAT II, 1980; GREAT III, 1982; and UMRBC, 1982). Habitat management and rehabilitation became a major thrust of these studies as biologists proposed new techniques such as opening and rehabilitating backwaters (Fremling et al. 1976, 1979; Nielsen et al. 1978), altering wing dikes and closing dams (Boland 1980; Grace and Weithman 1983; Pierce 1980), using larger rock for revetments (Farabee 1984), creating islands (Kennedy et al. 1979), protecting shorelines (Lovejoy and Kennedy 1979), and evaluating their effectiveness (Claflin and Rada 1979, 1980; Hall 1980; Talbot and Parsons 1985). Mitigation and enhancement techniques for the MR and other large rivers were compiled by Schnick et al. (1982).

In 1983, the UMRCC summarized potential habitat rehabilitation and enhancement projects for the UMR and Illinois rivers (Rasmussen 1983), estimating a need for at least $205M (1983 dollars) in habitat rehabilitation. Projects included backwater dredging, dike and levee construction, island creation, bank stabilization, side channel openings/closures, wing and closing dike modifications, aeration and water control systems, waterfowl nesting cover, acquisition of wildlife lands, and forest management. Public Law 99-662 (1986) authorized a $124.6-M, 10-yr habitat rehabilitation and enhancement program for the UMR System as part of the larger $190-M EMP, and this program is being implemented through an interagency (state and federal) effort.

The USACE (Lower Mississippi River Environmental Program) is developing environmental design considerations for navigation and flood control works on the LMR to improve habitat associated with levee borrow pits, dike systems, and revetments. Although none of these measures is specifically for fisheries management, some fish populations would be benefitted.

Stocking

Current UMR stocking efforts in Pool 14 by Iowa and Illinois include alternate year stocking of "wipers" and walleye (raised to fingerling stage in cooling ponds at the Cordova nuclear power plant) (Stoeckel 1985). The wiper is seen as a new trophy species that would utilize large gizzard shad; river-strain walleyes are being stocked to supplement natural reproduction. Stocking, however, has not and is not expected to be a major part of future river management. In 1981, the UMRCC Fish Technical Section prepared a position statement opposing maintenance stocking of native species as acceptable mitigation for deteriorating spawning and nursery habitat (UMRCC Ann. Proceed. 1982).

Management Problems

Unfortunately, the needs of fishery and waterfowl managers do not always coincide; conflicts over water-level requirements were summarized by Boyd and Harber (1981). Even though fisheries interests provided the initial justification for the first UMR refuge, the national interest in migratory waterfowl has taken precedence. Not until 1981 was a fisheries manager employed by the USFWS to develop fish management plans for UMR national wildlife refuges.

Public attitudes toward the river vary from north to south and are related to both biological and socioeconomic factors. Less-developed reaches offer aesthetic beauty and environmental benefits, while more-developed reaches may be aesthetically displeasing and unappreciated. Attitudinal differences are reflected in public investments in the river. On the UMR, for example, Illinois and Missouri share the longest river reaches and share in the largest investments in commercial navigation and its benefits; however, they employ the fewest river fisheries biologists of the upper five states. The same holds true for states along the MMR and LMR, where in some cases no state biologists are assigned river responsibilities. Further, virtually all public lands along the MR apparently are located in northern UMR reaches (UMR-1 through UMR-5) or along the AR, resulting in more apparent public interest in environmental preservation in those areas.

Effects of Cultural Intervention on Fish Resources

Detrimental effects of sedimentation in the UMR were recognized as early as 1930 by Ellis (1931). Soil conservation practices improved after the 1930s, but wetland drainage and stream channelization increased. Navigation pools, constructed during the 1930s, serve as sediment traps and experience average sedimentation rates up to 5 $\mathrm{cm \cdot yr.^{-1}}$. Within 50 yr, unless management action is taken, most of the UMR will consist of a main channel bordered by dry land, shallow marshes, and some running sloughs (UMRBC 1982).

Poor land management causes increased lowland flooding and has produced a need for flood protection levees, especially along the LMR and MMR. These levees have isolated the river and its fisheries from its floodplain in most areas, reduced flood storage capacity, and led to higher flood crests (Simons et al. 1975), thereby creating a need for more levees in previously unflooded areas and along the lower reaches of tributaries. Levees have encouraged development, and, as a result, fisheries habitat behind levees has been drained and filled. Flood control works have greatly decreased the amount of floodplain available as nursery, spawning, and feeding habitat. Further, many floodplain lakes have been isolated from river overflow and no longer serve as habitat for river fishes.

The growing environmental awareness of the 1960s and the subsequent enactment of NEPA, as well as the declining commercial fishery and worldwide concern for contamination of fish flesh, led to increased monitoring and restrictions on domestic and industrial effluents in the MR. Wiener et al. (1984) reported that concentrations of toxic trace elements (As, Cd, Cr, Hg, Pb, Se) in carp were generally highest upstream from, at, and immediately downstream from Minneapolis/St. Paul. Concentrations of Cd, Hg, and Pb in bed sediments were generally much higher and more enriched in Pools 1, 2, and 4 (Lake Pepin), which are at and downstream from Minneapolis/St. Paul. The Minneapolis/St. Paul area is the major source of PCB input as determined by monitoring of fish and sediments. Long-term studies of PCBs in fish from Pools 2–9 indicate a definite downward trend attributed to state and federal laws restricting discharge (Pers. commun. J. Sullivan, Wisc. Dept. Nat. Resour.). In 1986, however, Minnesota continued to issue warnings against consumption of large catfish and carp from Minneapolis/St. Paul to LaCrosse, Wisconsin (RKM 2 658) primarily because of PCB contamination (Minn. Dept. Health 1986). Missouri has issued similar warnings along its reach for chlordane contamination (Grace 1987).

Improved waste treatment facilities in the Minneapolis/St. Paul area have caused marked improvement in general water quality during the past decade, resulting in recurrence of *Hexagenia* mayflies (Fremling and Johnson 1988), increased fish diversity, and a more normalized comparative abundance of game and nongame fishes (pers. commun. J. Enblom, Minn. Dept. Nat. Resour.).

In the early 1960s, reports of fish kills in the LMR below Memphis and in the AR increased until state and federal pollution control agencies were asked to investigate the phenomena. In 1964, they recommended that endrin discharges from industry and land drainage be brought under control. A 3-yr study (1966–68) of the LMR and AR showed: (1) that endrin was slightly, but equally soluble at all river temperatures and toxic in concentrations from 10 to 40 $\mu g \cdot L^{-1}$; (2) that commercial species (marine and freshwater) were variously resistant and that some developed resistance; (3) that endrin concentrations peaked in 1964 and declined after the sources were pinpointed; (4) that no additional kills were reported after winter, 1964; (5) that fish community diversity had recovered by 1968 but that there was a paucity of larger size groups of long-lived species (Anonymous 1969).

Industrial and municipal discharges have increased in number for the past 15 years between St. Francisville (RKM 424) and Venice, Louisiana (RKM 16) (Everett 1971; Wells 1980; Romanowsky 1984). Currently, there are 130 industrial and 29 municipal discharges $\geq$ 50 000 gal$\cdot$day^{-1} on the lower 425 km of the LMR, 95 % of which are between Baton Rouge and New Orleans (La. Dept. of Environ. Qual. 1985). There are only 4 industrial and 6 municipal point-source discharges in the entire AR Basin. Discharges of lesser volume are not regarded as significant, either in number or impact.

Expanded use of the MR for commercial navigation has been a major political issue since the early 1900s (Scarpino 1985). Water-level fluctuations from pool management, tow traffic, and bed degradation have significant impacts on MR fisheries. Flow alterations and channelization lead to the filling of backwaters and main channel border habitats by enhancing the river's natural sediment sorting capabilities (Simons et al. 1975). Main channel sediments are primarily sand, while backwater sediments are composed of silt and are often contaminated with heavy metals, PCBs and pesticides. Most MR dredging is navigation-related and conducted in the main channel. Sand disposal on the UMR and MMR may cover more productive substrates and fill wetlands.

In Pool 5A (Anderson et al. 1983), 45 % of the original combined length of wing and closing dam structures has been lost either through burial or erosion. Sand was the dominant substrate in the main channel border of Pool 5A, underlying more than 70 % of the water surface area under low-flow conditions. Rock substrate was found only on the control structures, which underlie 5 % of the total water surface area.

Carmody et al. (1986) summarized the direct impacts of UMR commercial navigation, reporting that towboats scour the channel with their propellors, increase turbidity, erode shorelines, and entrain and impinge fish. Their barges pose the threat of toxic spills and may damage riparian and littoral habitats at fleeting areas.

Value of the Resource

Unlike most tropical rivers and much of the LMR, the HW and UMR are easily accessible by road and numerous launch ramps. Sport and commercial fishermen routinely use sonar and other sophisticated gear. The UMR alone provides over 30M activity days annually (UMRCC 1982). Using current figures (USFWS 1982) for recreational activity expenditures, UMR recreation contributes as much as $0.75B annually to the regional economy. Sport fishing on the UMR accounts for over 8.5M activity days/yr and $150–175M annually in first-market expenditures.

On the AR alone (there are no data for LMR) during 1971–74, there were annual averages of 0.97M daytime recreational trips valued at $42.4M (Soileau et al. 1975).

While conflicts between uses are inevitable, increased recreational use of the river should lead to increased awareness and increased concern for environmental protection. In the long run, therefore, recreational use of the MR should benefit most MR fish and wildlife interests.

Due to habitat loss, environmental contamination, and conflicts with navigation, the commercial fishery has been declining since 1970 (Table 6). Although commercial fishermen are trying to speak out (Rasmussen and Harber

1981), to become involved in political decisions, and to create new markets for their products (Cady and Ramer 1985), the industry as a whole is poorly organized.

Sport fishermen, on the other hand, are growing in strength. Their organizations are educating and organizing anglers, especially in the HW and UMR; they also have contributed money and equipment to state research efforts. Both sport and commercial fishing appear to be adequately regulated on the HW, UMR and MMR at the present time. Fishing regulations are far less restrictive on the LMR and AR but are considered adequate because the fishery seems to be accommodating the market.

Outlook for the Future

The long-term future for MR fisheries is not predictable, but the outlook for the next 10 yr is encouraging. The 1985 Farm Bill provided for 10- to 15-yr conservation reserves on highly erodible lands; up to 18.2M ha will be placed in this reserve annually through 1990. Most of the HW and UMR states have floodplain zoning laws in effect and in the future non-water-dependent developments will be difficult to locate there. Farm economics may even dictate that some levee and drainage districts be sold back to the government for fish and wildlife habitat. Navigation enhancement projects will be limited by the 1986 enactment of the Waterways Trust Fund whereby new expansion must be cost-shared by the industry. Over the next 10 yr, the EMP program will include: (1) long-term resource monitoring, (2) habitat rehabilitation and enhancement, (3) recreation improvements and studies, (4) navigation traffic monitoring, and (5) computerized inventory and analysis on the UMR and MMR (USACE 1985). MR resources will apparently be increasingly difficult to exploit without providing adequate mitigation.

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References

Ackelson, M. S. 1979. Recreational use survey, Pool 9, Mississippi River. Upper Miss. River Conserv. Committee Spec. Publ., Rock Island, IL. 36 p.

Ackerman, G. L, R. DeCook, P. E. Koehn, and B. J. Peterson. 1978. The potential for introducing striped bass (*Morone saxatilis*) into the Mississippi River. Ia. Conserv. Comm., Des Moines, IA. 28 p.

Adams, J. R. 1986. Mechanics of a large eddy in the Mississippi River. Proc. Am. Soc. Civ. Eng., Spec. Conf. on Advancements in Aerodynamics, Fluid Mechanics and Hydraulics. June 3–6, 1986. Minneapolis, MN. ASCE, 345 47th St., New York, NY

Anderson, D., D. Wilcox, D. McConville, and J. Smith, 1983. Physical and biological investigations of the main channel border (MCB) habitat of Pool 5A, on the Upper Mississippi River in 1980. USACE. St. Paul District, St. Paul, MN. 176 p.

Anderson, R. V., and D. M. Day. 1986. Predictive quality of macroinvertebrate-habitat associations in lower navigation pools of the Mississippi River. Hydrobiologia 136: 101–112.

Anonymous. 1969. Endrin pollution in the Lower Mississippi River. Basin. U.S. Fed. Wat. Pollut. Ctrl. Admin., S. Cent.Region, Dallas, TX. 125 p. + app.

Bahr, D. M. 1977. Homing, swimming behavior, range, activity patterns and reaction to increased water levels of walleye, (*Stizostedion vitreum vitreum*) as determined by radio-telemetry in Navigational Pools 7 and 8 of the Upper Mississippi River during Spring, 1976. M.S. thesis, Univ. Wis. LaCrosse, WI.

Bailey, P.A., and R.G. Rada 1984. Distribution and enrichment of trace metals (Cd, Cr, Cu, Ni, Pb, Zn) in bottom sediments of Navigation Pools 4 (Lake Pepin), 5, and 9 of the Upper Mississippi River, p. 119–138. *In* J. G. Wiener, R. V. Anderson and D. R. McConville [ed.] Contaminants in the Upper Mississippi River. Butterworth Publishers, Stoneham, MA.

Beck, L. T. 1977. Temporal and spatial distribution of benthic macroinvertebrates in the Lower Atchafalaya River Basin, Louisiana. M. S. thesis, School For. & Wildl. Mgmt., La. State Univ., Baton Rouge, LA.

Beckett, D.C., C.R. Bingham, L.G. Sanders, D.B. Mathis, and E.M. McLarmore. 1983. Benthic macroinvertebrates of selected aquatic habitats of the Lower Mississippi River. Tech. Report E-83-10, USACE, Waterways Exp. Station, Vicksburg, MI.

Beckett, D.C., and C.H. Pennington. 1986. Water quality, macroinvertebrates, larval fishes, and fishes of the Lower Mississippi. Mississippi River — a synthesis. USACE, Waterways Exp. Station, Vicksburg, MI. 137 p.

Bellrose, F.C., Jr., R.E. Sparks, F.L. Paveglio, Jr., D.W. Steffeck, R.C. Thomas, R.A. Weaver and D. Moll. 1977. Fish and wildlife habitat changes resulting from the construction of a nine-foot navigation channel in the Illinois Waterway from LaGrange Lock and Dam upstream to Lockport Lock and Dam. Report to USACE, Chicago Dist., Chicago, IL. 176 p.

Bhowmik, N.G., and J.R. Adams. 1986. The hydrologic environment of Pool 19 of the Mississippi River. Hydrobiologia 136: 21–30.

Binford, M. W. 1975. Crustacean zooplankton ecology of the Atchafalaya River Basin. Louisiana. M. S. thesis. School For. & Wildl. Mgmt., La. State Univ., Baton Route, LA.

Bingham, C. R. 1969. Comparative study of two oxbow lakes. Completion Report F-19-R, Mississippi Game and Fish Comm., Jackson, MI. 7 p.

Boland, T. L. 1980. A classification of the wing and closing dams on the Upper Mississippi River bordering Iowa. Report to Fish Wildl. Mgmt. Work Group, GREAT II, USACE, Rock Island Dist. Contr. No. DACW 25-79-C-0056: 55 p.

Boland, T. L., and G. L. Ackerman 1982. Investigations of tailwater walleye and sauger fisheries of the Upper Mississippi River. *In* 1982 Job Compl. Repts., Fish Mgmt. Branch, Iowa Conserv. Comm., Des Moines, IA. p. 120–148.

Boyd, W. and J. G. Harber [ed.]. 1981. Effects of fluctuating pool levels caused by normal operation of the Upper Mississippi River System 9-foot channel on wetland plants, waterfowl, muskrats, invertebrates and fish. Expert Panel Report for Upper Miss. River Basin Comm. Master Plan, Minneapolis, MN. 223 p.

Boyer, B. E. 1978. Distribution and relative abundance of fish eggs, larvae and early juveniles in the inundated Mississippi

River floodplain near St. Francisville, Louisiana. M. S. thesis, School For. & Wildl. Mgmt., La. State Univ., Baton Rouge, LA.

BRYAN, C. F., J. V. CONNOR, AND D. J. DEMONT. 1974a. An ecological study of the Lower Mississippi River and waters of the Gulf States property near St. Francisville, Louisiana. I and II. *In* Environmental Report River Bend Sect. Atomic Energy Comm., Vol. III and IV. App. E.

BRYAN, C. F., D. R. DEMONT, AND D. S. SABINS. 1977. Habitat evaluation procedures: application in aquatic habitats and communities of the Atchafalaya Basin. Fourth Annu. Report, U. S. Fish. Wildl. Serv., Div. Ecol. Serv., St. Louis, MO.

BRYAN, C. F., AND D. S. SABINS. 1978. Management implications in water quality and fish standing stock information in the Atchafalaya River Basin, La. Proc. 3rd Coastal Marsh and Estuary Mgmt. Sym., La. State Univ., March, 1978.

BRYAN, C. F., F. M. TRUESDALE, AND D. S. SABINS. 1975. Limnological studies of the Atchafalaya Basin and Atchafalaya Bay. U. S. Dept. of Interior, Washington, D. C. pp 43–95.

BRYAN, C. F., F. M. TRUESDALE, D. S. SABINS, AND C. R. DEMAS. 1974b. A limnological survey of the Atchafalaya Basin. A progress report. U. S. Dept. of Interior, Washington, D. C.

BRYAN, C. F., F. M. TRUESDALE, B. S. SABINS, AND J. T. NEWMAN, JR. 1976. Limnological survey of the Atchafalaya Basin and Atchafalaya Bay. U. S. Dept. Interior. Washington D. C.

BUTTS, R.A., R.L. EVANS, AND R.E. SPARKS. 1982. Sediment oxygen demand — fingernail clam relationship in the Mississippi River Keokuk Pool. Trans. Ill. Acad. Sci. 75 (1 and 2): 29–30.

CADY, J., AND H. RAMER. 1985. Innovative approaches to utilizing and marketing the Mississippi River carp resource, p. 99–106. *In* Proc. 41st. Annu. Meet. Upper Miss. River Conserv. Committee, Rock Island, IL.

CAHILL, R.A., AND A.D. AUTREY. 1987. Measurement of 210Pb, 137Cs, organic carbon and trace elements in sediments of the Illinois and Mississippi rivers. J. Radioanal. Nuclear Chem. 110(1): 197–205.

CAHILL, R.A., A.D. AUTREY, R.V. ANDERSON, AND J.W. GRUBAUGH. 1987. Improved measurement of the organic carbon content of various river components. J. Freshwater Ecol. 4:423–428.

CARLANDER, H.B. 1954. A history of fish and fishing in the Upper Mississippi River. Upper Miss. River Conserv. Committee, Spec. Publ., Rock Island, IL. 96 p.

CARLSON, D.D., G.R. STALWORTH, L.J. DANTIN, AND C.G. STUART. 1982. Water resources data. U.S. Geol. Surv., Baton Rouge, LA. Vol 2. 404 p.

1983. Water resources data. Vol. 2. U.S. Geol. Surv., Baton Rouge, LA. Vol 2, 360 p.

1984. Water resources data. Vol. 2. U.S. Geol. Surv., Baton Rouge, LA. Vol 2, 608 p.

CARMODY, G.A., L.E. HOLLAND, AND J.L. RASMUSSEN. 1986. General impacts of navigation traffic on the Upper Mississippi River system (UMRS). Contr. Report for USACE, St. Louis Dist., St. Louis, MO. 116 p.

CLAFLIN, T.O., AND R.G. RADA. 1979. A field test of the regression simulation model in Fountain City Bay, Wisconsin. USACE, St. Paul Dist., Final Report Contr. No. DACW-37-77-C-0136, St. Paul, MN.

1980. A study of effects of diverting water into Upper Burnt Pocket, Navigation Pool No. 18, Illinois, and a field test of the regression simulation model previously developed on Navigation Pool No. 8. Final report USACE, Rock Island Dist., Contr. No. DACW-25-78-C-0047, Rock Island, IL.

CLAFLIN, T. O., R. G. RADA, M. M. SMART, D. N. NIELSEN, J. K. SCHEIDT, AND B. A. BILTGEN. 1981. The effects of commercial and recreational navigation on selected physical and chemical variables in Navigation Pool No. 9, Upper Mississippi River. Report submitted to Upper Mississippi River Basin Comm., St. Paul, MN.

CLARY, P. 1985. Habitat characteristics and food of larval black crappie (*Pomoxis nigromaculatis*) and warmouth (*Lepomis gulosus*) in selected overflow habitats of the Atchafalaya River basin, Louisiana. M. S. thesis, La. St. Univ., Baton Rouge, LA. 56 p.

CLARY, P., AND C. F. BRYAN. 1985. Value of ichthyoplankton in the characterization of Lower Atchafalaya Basin habitat. Poster Pap. Annu. Larval Fish Conf., Port Aransas, TX.

COBB, S. P. 1988. An aquatic macrohabitat classification for the Lower Mississippi River with the effects of river stage on habitat size. Can. J. Fish. Aquat. Sci. (In press).

COBB, S. P., AND J. R. CLARK. 1981. Aquatic habitat studies on the Lower Mississippi River, river mile 480–530. Report 2, aquatic habitat mapping. Misc. Paper E-80-1, USACE, Waterways Exp. Sta., Vicksburg, MS. 23 p. + tables.

COBB, S. P., C. H. PENNINGTON, J. A. BAKER, AND J. E. SCOTT. 1984. Fishery and ecological investigations of main-stem levee borrow pits along the Lower Mississippi River. Lower Mississippi River Environ. Program Report 1, Mississippi River Comm., Vicksburg, MS. 93 p. and tables.

COBB, S. P., AND A. D. MAGOUN. 1985. Physical and hydrologic characteristics of aquatic habitat associated with dike systems in the Lower Mississippi River. Lower Mississippi River Environ. Program Report 5, Miss. River Comm., Vicksburg, MS. 72 p. + tables.

COKER, R. E. 1913. Water-power development in relation to fishes and mussels of the Mississippi. Report U. S. Comm. Fisheries for 1913. App. VIII. 28 p., 5 plates.

1930. Studies of common fishes of the Mississippi River at Keokuk, 1930. Bur. Fish. Doc. 1072, Bull. Bur. Fish. 45: 141–225.

CONNER, J. V. 1982. Fishes known to occur in the Mississippi River and/or tributaries near St. Francisville, Louisiana. La. St. Univ. Fish. Museum Checklist (mimeo).

CONNER, J. V., R. P. GALLAGHER, AND M. F. CHATRY. 1980. Larval evidence for natural reproduction of the grass carp (*Ctenopharyngodon idella*) in the Lower Mississippi River, p. 1–19. *In* L. E. Fuiman [ed.] Proc. 4th Annu. Larval Fish Conf., Univ. Michigan, Ann Arbor, MI.

CONNER, J. V., C. H. PENNINGTON, AND T. R. BOSLEY. 1983. Larval fish of selected aquatic habitats on the Lower Mississippi River. Tech. Report E-83-4. USACE Waterways Exp. Sta., Vicksburg, MS. 30 p. + tables.

DUNHAM, L. L. 1971. Fish sampling by electro-fishing gear below navigation dams 12–26 on the Mississippi River. Ill. Dept. Conserv., Div. Fish, Springfield, IL. (mimeo).

ECOLOGICAL ANALYSTS, INC. 1984. Aquatic studies of the main channel border habitat of Pool 5A on the Upper Mississippi River. USACE, St. Paul Dist., St. Paul, MN. 309 p.

EDDY, S., J. B. MOYLE, AND J. C. UNDERHILL. 1963. The fish fauna of the Mississippi River above St. Anthony Falls as related to the effectiveness of this falls as a migration barrier. Proc. Minn. Acad. Sci. 32(2): 111–115.

EDDY, S., AND J. C. UNDERHILL. 1974. Northern fishes. 3rd ed. Univ. of Minn. Press, Minneapolis, MN. 414 p.

ELLIS, M. M. 1931. A survey of conditions affecting fisheries in the Upper Mississippi River. U.S. Bur. Fish. Circ. 5: 1–18.

ENBLOM, J. W. 1977. A biological reconnaissance of the Upper Mississippi River, St. Cloud to Fridley. Minn. Dept. Nat. Resources, Div. Fish Wildl., Ecol. Serv. Spec Publ. No. 121. St. Paul, MN. 81 p.

ENGMAN, J. A. 1984. Phytoplankton distribution in Pool 19, Mississippi River. M. S. thesis, W. Ill. Univ. Macomb, IL. 113 p.

ENVIRONMENTAL SCIENCE AND ENGINEERING, INC. 1982. Final Report, GREAT III Ecological and Habitat Characterization.

Prep. for USACE, St. Louis Dist., ESE No. 81-803-860. Contr. No DACW 43-81-C-00065, St. Louis MO.

Everett, D. E. 1971. Hydrologic and quality characteristics of the Lower Mississippi River. La. Dept. Public Works, U. S. Geol.Surv., Baton Rouge, LA. Tech. Rep. No. 5, 48 p.

Fairchild, M. 1982. The legal and administrative history of the Upper Mississippi River Wildlife and Fish Refuge. U. S. Fish Wildl. Serv., Winona, MN. mimeo.

Farabee, G. B. 1980. Tailwater Creel Census, Pool 24, Mississippi River, May 20–Sept. 26, 1980. Fish Mgmt. Report, Mo. Dept. Conserv., Jefferson City, MO. 8 p.

1984. Final report on electrofishing data collected from revetted and natural shoreline—Mississippi River, river miles 288, 289, 291 and 294. Mo. Dept. Conserv., Palmyra, MO. 5 p.

Fenneman, N. M. 1938. Physiography of the Eastern United States. McGraw-Hill Book Co., Inc., New York, NY. 714 p.

Finke, A. H. 1966a. White bass tagging study, Upper Mississippi River, 1964. Fish. Mgmt. Div. Report, Wisconsin Conserv. Dept., Madison, WI. 11 p., mimeo.

1966b. Northern pike tagging study, Black River, LaCrosse Co., WI, 1964–1965. Wis. Conserv. Dept. Report No. 7. Madison, WI. 4 p.

Fisk, H. N. 1944. Geological investigation of the alluvial valley of the Lower Mississippi River. Miss. River Comm., Vicksburg, MS. 78 p.

1952. Mississippi River valley geology relation to river regime. Trans. Am. Soc. Civil Eng., 117, No. 2511: 667–689.

Fleener, G. G. 1975. The 1972–73 sport fishery survey of the Upper Mississippi River. Upper Miss. River Conserv. Committee Spec. Publ., Rock Island, IL. 28 p + app. A–B.

1976. Recreational use of Pool 21, Mississippi River. Upper Miss. River Conserv. Committee Spec. Publ., UMRCC, Rock Island, IL. 21 p. + app.

Fossum, J. D. 1975. Age and growth, food habits analysis, and movement patterns of walleye, (*Stizostedion vitreum vitreum*), (Mitchell) in Pools 3 and 4 of the Upper Mississippi River. M.S. thesis, St. Mary's Coll., Winona, MN.

Frazier, D. E. 1967. Recent deposits of the Mississippi River, their development and chronology. Trans. Gulf Coast Assoc. Geolog. Soc. 17: 287–311.

Fremling, C. R. 1980. *Aplodinotus grunniens* (Raf.), Freshwater drum., p. 756. *In* D. S. Lee et al.[ed.], Atlas of N. Amer. freshwater fishes. N.C. State Mus. Nat. Hist., Raleigh, NC. ix + 854 p.

1987. Human impacts on Mississippi River ecology. Proc. 10th. Nat. Coast. Soc. Conf., New Orleans, LA., 1986. p. 235–240.

Fremling, C. R., and T. O. Claflin. 1984. Ecological history of the Upper Mississippi River. p. 5-24. *in* J. G. Wiener, R. V. Anderson, and D. R. McConville, [ed.], Contaminants in the Upper Mississippi River. Proc. 15th Annu. Meet. Miss. River Res. Consort. Butterworth Publishers, Stoneham, MA.

Fremling, C. R., and D. K. Johnson. 1988. Recurrence of *Hexagenia* mayflies demonstrates improved water quality in Pool 2 and Lake Pepin, Upper Mississippi River. Proc. 5th Intl. Conf. on Ephemeroptera. (in press)

Fremling, C. R., D. N. Nielsen, and D. R. McConville. 1976. The Weaver Bottoms: a field model for the rehabilitation of backwater areas of the Upper Mississippi River by modification of standard channel maintenance practices. Prep. for USACE, St. Paul Dist. Winona St. Univ., Winona, MN., Contr. No. DACW 37-75-C-0193, and St. Mary's Coll., Winona, MN., Contr. No. DACW 37-74-C-0194. St. Paul, MN. 302 p.

Fremling, C. R., D. N. Nielsen, D. R. McConville, R. N. Vose, and R. Faber. 1979. The feasibility and environmental effects of opening side channels in five areas of the Mississippi River (West Newton Chute, Fountain City Bay, Sam Gordy's Slough, Kruger Slough and Island 42). Vol. I, II. U.S. Fish and Wildl. Serv., Twin Cities, MN. Contr. No. 14-16-0008-949. 298 p.

Gagliano, S. M., and P. C. Howard. 1984. The neck-cutoff oxbow lake cycle along the Lower Mississippi River, p. 147–158. *In* C. M. Elliot [ed.] River Meandering. Am. Soc. Civil Eng., New York, NY.

Gale, W. F. 1969. Bottom fauna of Pool 19, Mississippi River with emphasis on the life history of the fingernail clam, *Sphaerium transversum*. Ph.D. dissertation, Ia. St. Univ., Ames, IA. 234 p.

Gallagher, R. P., and J. V. Conner. 1980. Spatio-temporal distribution of ichthyoplankton in the Lower Mississippi River, Louisiana. *In* L. A. Fuiman [ed.] Proc. 4th Annu. Larval Fish Conf. U. S. Fish and Wildl. Serv. Biol. Services Prog., WS/OB-84/43, Ann Arbor, MI. 179 p.

Gengerke, T. W. 1978. Paddlefish investigations. Proj. Compl. Report Res. Segments 1–3. Ia. Conserv. Comm., Des Moines, IA.

Gilbertson, D. E., and T. J. Kelly. 1981. Summary resource description: Upper Mississippi River system. Vol. 4 Biology. Contract Report. Upper Miss. River Basin Assoc., 415 Hamm Bldg., 408 St. Peter St., St. Paul, MN. 102 p.

Glasgow, L. L., and R. E. Noble. 1974. The Atchafalaya Basin. School For. & Wildl. Mgmt., La. State Univ., Baton Rouge, LA. 12 p. (mimeo).

Goff, Prilesnitz and Associates. 1981. A management plan for the Upper Mississippi River. Prepared for the Miss. Headwaters Bd. Twin Cities, MN. 38 p. 79 maps.

Grace, T. B. 1987. Pesticide levels in fish from the Missouri and Mississippi Rivers in Missouri. *In* Proc. Annu. Meet. Upper Miss. Riv. Conserv. Committee, Rock Island, IL.

Grace, T. B., and A. J. Weithman. 1983. Influence of channel regulating structures on fish and macroinvertebrates in the Middle Mississippi River, p. 137–140. *In* Proc. 39th Annu. Meet. Upper Miss. River Conserv. Committee, Rock Island, IL.

Grady, J. M., R. C. Cashnere, and J. S. Rogers. 1983. Fishes of the Bayou Sara drainage, Louisiana and Mississippi, with discriminant functions analyses of factors influencing species distribution. Tulane Studies in Zool. and Bot., Vol 24 No. 2. p. 83–100.

Great I. 1980. A Study of the Upper Mississippi River. 9 vols. USACE, St. Paul Dist., St. Paul, MN.

Great II. 1980. Great II main report and appendices. USACE, Rock Island Dist., Rock Island, IL.

Great III. 1982. Great River Resour. Management Study — 14028. USACE, St. Louis Dist., St. Louis, MO. 78 p.

Greenbank, J. 1946. Effects of midwinter drawdowns of the Upper Mississippi River on aquatic wildlife, p. 17–24. *In* K. D. Keenlyne [ed.]. 1974. Upper Miss. River Conserv. Committee, Invest. Repts. Rock Island, IL.

1957. Creel census on the Upper Mississippi River. U.S. Fish Wildl. Serv. Spec. Sci. Report, Fish. No. 202: 59 p.

Grubaugh, J. W., and R. V. Anderson 1988. Seasonal fluxes and the influences of floodplain forest on organic matter dynamics in the Upper Mississippi River. Hydrobiologia (in press).

Grubaugh, J. W., R. V. Anderson, D. M. Day,. and K. S. Lubinski. 1986. Production and fate of organic material from *Sagittaria latifolia* and *Nelumbo lutea* on Pool 19, Mississippi River. J. Freshwater Ecol. 3: 477–484.

Grunwald, G. L. 1983. Modification of alternating current electrofishing gear for deep water sampling. Minn. Dept. Nat. Resources, Fish Mgmt. Report No. 10, p. 177–187. *In* Proc. 39th Annu. Meet. Upper Miss. River Conserv. Committee, Rock Island, IL.

Guillory, V. 1982. Fishes of the Lower Mississippi River near

St. Francisville, Louisiana. Proc. La. Acad. Sci. XLV: 108–121.

HALL, T. J. 1980. Influence of wing dam notching on aquatic macroinvertebrates in Pool 13, Upper Mississippi River, the pre-notching study. M.S. thesis, Univ. Wisc., Steven's Point, WI. 168 p.

HALLBERG, R. R., E. A. BETTIS III, AND J. C. PRIOR. 1984. Geological overview of the paleozoic plateau region of northeastern Iowa. Proc. Iowa. Acad. Sci. 91(1): 5–11.

HARRIS, G. P., AND B. B. PICCINIA. 1977. Photosynthesis by natural phytoplankton populations. Arch. Hydrobiol. 80: 405–457.

HARTZOG, L. M. 1975. Physiochemical characteristics of the Lower Mississippi River at St. Francisville, Louisiana. M.S. thesis, Louisiana St. Univ., Baton Rouge, LA. 81 p.

HATCHER, R. M. N. D. Endangered or extinct — the difference could be you. Publ. Tenn. Wildl. Resources Agency. Nashville TN. 6 p.

HAWKINSON, B., AND G. GRUNWALD. 1979. Observation of a wintertime concentration of catfish in the Mississippi River. Minn. Dept. Nat. Resources Invest. Report No. 365. St. Paul, MN. 13 p.

HEBERT, K. L. 1967. The flood control capabilities of the Atchafalaya Basin floodway. La. Wat. Resour. Res. Inst., La. St. Univ., Baton Rouge, LA.

HELMS, D. R. 1969. Fifteen-inch size limit proposal for channel catfish in the Mississippi River. Iowa Conserv. Comm. Quart. Biol. Repts. Oct.-Dec. Des Moines, IA. 6 p.

1975. Variations in the abundance of channel catfish year classes in the Upper Mississippi River and causative factors. Iowa Conserv. Comm., Tech. Serv. 75-1, Dec. 1975. 31 p.

HENEBRY, M. S., AND R. W. GORDEN. 1988. Bacterial production in Mississippi River Pool 19. Appl. Environ. Microbiol. (in press).

HOCUTT, C. H., AND E. O. WILEY. 1986. The zoogeography of North American freshwater fishes. John Wiley & Sons, New York, NY.

HOLLAND, L. E. 1986. Distribution of early life stages of fishes in selected pools of the Upper Mississippi River. Hydrobiologia 136: 121–130.

HOLLAND, L. E., C. F. BRYAN, AND J. P. NEWMAN, JR. 1983a. Water quality and the rotifer populations in the Atchafalaya River Basin. Hydrobiologia 98: 55–69.

HOLLAND, L. E., D. HUFF, S. LITTLEJOHN, AND R. JACOBSEN. 1984. Analysis of existing information on adult fish movements through dams on the Upper Mississippi River. Contr. Report Prep. for USACE, St. Paul District, St. Paul, MN.

HOLLAND, L. E., AND M. L. HUSTON. 1983. A compilation of available literature on the larvae of fishes common to the Upper Mississippi River. Contr. Report Prep. for USACE, Rock Island Dist., under Letter Order NCR-LO-83-C9, Rock Island, IL. 364 p.

HOLLAND, L. E., M. L. HUSTON, AND T. W. KAMMER. 1983b. Assemblages of larval fishes in various border habitats in the Upper Mississippi River. Prog. Report, Nat. Fish. Res. Lab., La Crosse, WI. 15 p. (mimeo.)

HOLLAND, L. E., AND J. R. SYLVESTER. 1983. Distribution of larval fishes related to potential navigation impacts on the Upper Mississippi River, Pool 7. Trans. Am. Fish. Soc. 112(2B): 293–301.

HOLZER, J. A. 1980. Determining the significance of wing dams, riprap and sand as fishery habitat, p. 18–28. *In* Miss. River Work Unit Annu., Report 1978–80. Wis. Dept. Nat. Resources, LaCrosse, WI.

HOLZER, J. A., AND K. L. VON RUDEN. 1984. Determining walleye spawning movements in Pool 8 of the Mississippi River. p. 1–78. *In* Miss. River Work Unit Annu., Report 1982–83. Wis. Dept. Nat. Resources, LaCrosse, WI.

HURLEY, W. A., AND L. G. NICKUM. 1983. Habitat associations and movements, with reference to spawning of shovelnose sturgeon in Pool 13 of the Upper Mississippi River. Proj. Comp. Report, Ia. Coop. Fish. Res. Unit, Ia. St. Univ., Ames, IA. 79 p.

HYNES, H. B. N. 1970. The ecology of running waters. Univ. Toronto Press, Toronto, Ont. 555 p.

ISERI, K. T., AND W. B. LANGBEIN. 1984. Large rivers of the United States. Geol. Sur. Circ. No. 686, Nat. Ctr., Reston, VA. 10 p.

JACKSON, G. A., C. E. KORSCHGEN, P. A. THIEL, J. M. BESSER, D. W. STEFFECK, AND M. H. BAKENHAUER. 1981. A long-term resource monitoring plan for the Upper Mississippi River System. Report Prep. for Upper Miss. River Basin Comm., Bloomington, MN. Vols. I & II.

JENKINS, R. E., E. A. LACHNER, AND F. J. SCHWARTZ. 1972. Fishes of the central Appalachians drainage: their distribution and dispersal. *In* T. C. Holt [ed.] The distributional history of the biota of the southern Appalachians. Part III. The Vertebrates. Va. Poly. Inst. & St. Univ., Res. Div. Monogr. 4, Blacksburg, Va.

JOHNSON, M. W. 1968. A fisheries survey of the Mississippi River, Grand Rapids to Brainerd, MN, 1965–67. Minn. Dept. Conserv. Spec. Publ. No. 61: 39 p.

JUDE, D. J. 1968. Bottom fauna utilization and distribution of 10 species of fish in Pool 19, Mississippi River. M.S. thesis, Ia. State Univ., Ames, IA. 239 p.

1973. Food and feeding habits of gizzard shad in Pool 19, Mississippi River. Trans. Am. Fish. Soc. 102(2): 378–383.

KELLEY, J. 1965. A taxonomic checklist of the fishes of Delta National Wildlife Refuge with emphasis upon distribution and abundance. M. S. thesis, Louisiana St. Univ., Baton Rouge, LA. 133 p.

KENNEDY, D. M., J. HOLZER, P. THIEL, T. LOVEJOY, B. HAWKINSON, N. GULDEN, AND R. NICKLAUS. 1979. Experimental island creation for fish and wildlife enhancement. App. to Fish and Wildl. Work Group Report, Great River Environ. Action Team. USACE, St. Paul Dist., St. Paul, MN.

KEOWN, M. P., E. A. DARDEAU, JR., AND E. M. CAUSEY. 1981. Characterization of the suspended-sediment regime and bedload gradation of the Mississippi River Basin. Report 1, Vols. 1 and 2. Environ. Lab., USACE, Waterways Exp. Station, Vicksburg, MS.

KLINE, D. R., AND J. L. GOLDEN. 1979a. Analysis of the Upper Mississippi River commercial fishery, p. 82–117. *In* J. L. Rasmussen, A Compendium of Fishery Information on the Upper Mississippi River. Upper Miss. River Conserv. Committee, Spec. Publ., Rock Island, IL.

1979b. Analysis of the Upper Mississippi River sport fishery between 1962 and 1973, p. 69–81. *In* J. L. Rasmussen, A Compendium of Fishery Information on the Upper Mississippi River. Upper Miss. River Conserv. Committee, Spec. Publ. Rock Island, IL.

KUCERA, T. A., AND A. R. PETERSON. 1980. Fish and wildlife resources of the Mississippi River from Lake Itasca to Lake Winnibigoshish. Minn. Dept. Nat. Resources, Spec. Publ. No. 129: 83 p.

LAMBOU, V. M. 1959. Fish populations of backwater lakes in Louisiana. Trans. Am. Fish. Soc. 88: 7–15.

LANE, E. W. 1957. A study of the shape of channels formed by natural streams flowing in erodible material. Mo. Riv. Div. Sed. Serv. No. 9, USACE, Missouri River Division, Omaha, NB.

LANTZ, K. 1974. Natural and controlled water level fluctuation in a backwater lake and three Louisiana impoundments. La. Wildl. & Fish. Comm., Fish. Bull. No. 11: 36 p.

LARSON, T., AND R. G. RANTHUM. 1977. The effects of commercial fishing through the ice on a winter congregation of channel catfish (*Ictalurus punctatus*) and flathead catfish

(*Pylodictis olivaris*) in Pool 7 of the Mississippi River. Fish Mgmt. Report Wis. Dept. Nat. Resources, W. Cent. Dist., La Crosse, WI.

Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister, and J. R. Stauffer, Jr. 1980. Atlas of North American fishes. N. Carolina Biol. Surv. 854 p.

Leidy, G. R., and R. M. Jenkins. 1977. The development of fishery compartments and population rate coefficients for use in reservoir ecosystem modeling. Contr. Report Y-77-1. USDI Fish and Wildl. Serv. Fayetteville, AR. and USACE Waterway Exp. Stat., Vicksburg, MS. 72 p. + app.

Les, B. L. 1979. The vanishing wild — Wisconsin's endangered wildlife and its habitat. Wis. Dept. Nat. Resources, Madison, WI 35 p.

LGL Ecological Research Associates, Inc. 1981. Study of fish in the main channel of the Mississippi River between river miles 500 and 512.5. Prepared for GREAT II Fish and Wildl. Mgmt. Work Group, U. S. Fish and Wildl. Serv., Rock Island, IL. and USACE, Rock Island, IL.

Livingstone, D. A. 1963. Chemical composition of rivers and lakes, p. G1–G64. *In* Data of Geochemistry (6th ed.): U.S. Geol. Surv. Prof. Pap. 440-G.

Louisiana Dept. of Environmental Quality. 1985. Louisiana water quality management basin atlas. Off. Wat. Resources. Wat. Pollut. Ctrl. Div., Baton Rouge, LA. 10 p. + app.

Lovejoy, T. A., and D. M. Kennedy. 1979. Shoreline protection for habitat enhancement on the Upper Mississippi River. App. to Fish and Wildlife Work Group Report, Great River Environmental Action Team. USACE, St. Paul District, St. Paul, MN.

Lower Mississippi Region Comprehensive Study Coordinating Committee. 1974. Lower Mississippi region comprehensive study (in 22 volumes), U. S. Govt. Printing Off., Washington, D. C.

Lubinski, K. S. 1984. Winter diving surveys of main channel microhabitats and fish populations in Mississippi River reaches subjected to thalweg disposal. Aquat. Biol. Tech. Report 13. Ill. Nat. Hist. Surv. Prep. for USACE, Rock Island Dist., Rock Island, IL 41 p.

Lubinski, K. S., M. J. Wallendorf, and M. C. Reese. 1981. Analysis of the Upper Mississippi River system — correlations between physical, biological and navigation variables. Upper Miss. River Basin Assoc. 415 Hamm Bldg., 408 St. Peter St., St. Paul, MN. 50 p.

Lubinski K. S., A. Van Vooren, G. Farabee, J. Janecek, and S. D. Jackson. 1986. Common carp in the Upper Mississippi River. Hydrobiologia 136: 141–154.

Mauck, W. L., and L. E. Olson. 1977. Polychlorinated biphenyls in adult mayflies (*Hexagenia bilineata*) from the Upper Mississippi River. Bull. Environ. Contam. Toxicol. 17: 387–390.

Miller, R.R. 1965. Quaternary freshwater fishes of North America, p. 569–581. *In* H. E. Wright, Jr. and D. G. Frey [ed.] The Quaternary of the United States. Princeton Univ. Press, Princeton, NJ.

Minnesota Department of Health. 1986. Minn. Fish Consumption Advisory, May, 1986. St. Paul, MN.

Mississippi River Work Unit. 1976. Evaluation of sonar sounding equipment. *In* Miss. River Work Unit Accomplishment Report Wis. Dept. Nat. Resources, La Crosse, WI.

1977. Winter sonar scanning, Pool 7, Mississippi River. *In* Miss. River Work Unit Annu. Report 1976–77. Wis. Dept. Nat. Resources, La Crosse, WI.

1979. Winter SCUBA observations of catfish aggregations in Pool 4, Mississippi River. (cooperative effort with Minnesota DNR). *In* Miss. River Work Unit Annu. Report 1978–79. Wis. Dept. Nat. Resour. La Crosse, WI.

1980. Mississippi River spring tailwater sport fishing creel census in Pools 7, 8 and 9. *In* Mississippi River Work Unit Annu. Report, 1979–80. Wis. Dept. Nat. Resources, LaCrosse, WI.

Moyle, J. B. 1975. The uncommon ones — animals and plants which merit special consideration and management. Minn. Dept. Nat. Resour. Spec. Publ. 32 p.

Moyle, J.B., and J. J. Cech, Jr. 1982. Fishes: an introduction to ichthyology. Prentice Hall, Inc., Englewood Cliffs, NJ.

Natural Land Institute. 1981. Endangered and threatened vertebrate animals and vascular plants of Illinois. Ill. Dept. Conserv., Springfield, IL. 189 p.

Nielson, D. N., C. R. Fremling, R. N. Vose, and D. R. McConville. 1978. Phase I study of the Weaver-Belvidere area, Upper Miss. River Contr. No. 14-16-0003-77-060. U. S. Fish Wildl. Serv., Twin Cities, MN. 234 p.

Nord, R. C. 1964. The 1962–1963 sport fishery survey of the Upper Mississippi River. Upper Miss. River Conserv. Comm. Spec. Publ., Rock Island, IL. 209 p.

Nordstrom, G. R., W. L. Pflieger, K. C. Sadler, and W. H. Lewis. 1977. Rare and endangered species of Missouri. Mo. Dept. Conserv., Jefferson City, MO, and USDA-SCS Spec. Publ. 129 p.

Nunnaly, N. R., and L. Beverly. 1984. Morphological effects of Lower Mississippi River dike fields. p. 418–429. *In* C. M. Elliot [ed.] River Meandering. Proc. Conf. Rivers 1983, ASCE, New York, NY.

Olson, K. N., and M. P. Meyer. 1976a. Vegetation, land, and water surface changes in the upper navigable portion of the Mississippi River Basin over the period 1939–1973. Univ. Minn., Institute of Agriculture, Forestry, and Home Economics, Remote Sensing Laboratory, Research Report No. 76-4. 225 p.

1976b. Vegetation, land, and water surface changes in the upper navigable portion of the Mississippi River Basin over the period 1929–1973. Univ. Minn., Inst. of Agriculture, Forestry, and Home Economics, Remote Sensing Laboratory, Research Report No. 76-5. 100 p.

Penland, S., and R. Boyd. 1985. Mississippi delta shoreline development, p. 53–115. *In* S. Penland and R. Boyd [ed.] Transgressive Depositional Environments of the Mississippi River Delta Plain: A Guide to Barrier Islands, Beaches and Shoals in Louisiana. La. Geol. Surv., Baton Rouge, LA.

Pennington, C. H., J. A. Baker, and C. L Bond. 1983. Fishes of selected aquatic habitats on the Lower Mississippi River. Tech. Report E-83-2, USACE, Waterways Exp. Sta., Vicksburg, MS. 65 p. + tables.

Pennington, C. H., H. L. Schramm, Jr., M. E. Potter, and M. P. Farrell. 1980. Aquatic habitat studies on the Lower Mississippi River, river mile 480–530; Report 5, fish studies pilot report. Miscell. Paper E-80-1, USACE, Waterways Exp. Sta. Vicksburg, MS. 45 p + app.

Pflieger, W. L. 1975. The fishes of Missouri. Mo. Dept. Conserv., Jefferson City, MO. 343 p.

Pierce R. B. 1980. Upper Mississippi River wing dam notching: the prenotching fish study. M.S. thesis, Univ. Wisconsin, Stevens Point, WI. 269 p.

Pitlo, J. M. 1981. Wing dam investigations. Iowa Conserv. Comm. Commercial Fish. Invest., Project Compl. Report Proj. No. 2-350-R. Ia. Conserv. Comm., Des Moines, IA. 145 p.

1985. Walleye and sauger use of wing and closing dam habitat as determined by radio telemetry. Fed. Aid to Fish Restoration, Proj. F-96-R-1. Job 1-3, Ia. Conserv. Comm., Des Moines, IA.

1987. Standing stock estimates of Upper Mississippi River habitats. Special Upper Miss. Riv. Conserv. Committee Spec. Publ. (In press).

Platner, W. S. 1946. Water quality studies of the Mississippi River, p. 77. *In* U.S. Fish Wildl. Serv. Spec. Sci. Report No. 30.

Ranthum, R. G. 1969. The food habits of several species of fish from Pool 19. Mississippi River. M. S. thesis. Ia. St. Univ., Ames, IA. 207 p.

Rasmussen, J. L. 1979. A compendium of fishery information on the Upper Mississippi River. 2nd ed. Upper Miss. River Conserv. Committee Spec. Publ., Rock Island, IL. 259 p.

1983. Habitat rehabilitation and enhancement projects Upper Miss. River Conserv. Committee, Memo to UMRCC Executive Board, Aug. 16, 1983. 10 p.

1984. Experimental primacord detonation to sample fish populations of Upper Mississippi River (UMR) main channel border habitat, p. 49–67. *In* Proc. 40th Annu. Meet. Upper Miss. River Conserv. Committee, Rock Island, IL 61201.

Rasmussen, J. L., and J. G. Harber [ed.]. 1981. Effects of navigation and operation and maintenance of the Upper Mississippi River System 9-foot channel on commercial fish and fishing. Expert Panel Report for the Environ. Work Team, Upper Miss. Riv. Basin Comm. Master Plan, Minneapolis, MN. 100 p. + app.

Rasmussen, J. L., J. Pitlo, and A. Van Vooren. 1985. Use of primacord to sample fish populations of Upper Mississippi River (UMR) main channel border habitat. Contr. Report Prep. for USACE, Rock Island Dist., Rock Island, IL. 35 p. + app.

Richardson, R. E. 1921. The small bottom and shore fauna of the Middle and Lower Illinois River and its connecting lakes, Chillicothe to Grafton: its valuation; its sources of food supply; and its relation to the fishery. Ill. Nat. Hist. Surv. Bull. 13(15): 363–522.

Risotto, S. P., and R. E. Turner. 1985. Annual fluctuation in abundance of the commercial fisheries of the Mississippi River and tributaries. N. Am. J. of Fish. Mgmt. 5: 557–574.

Robins, C. R., R. M., Bailey, C. E. Bond, J. R. Brooker, E. A. Lochner, R. N. Lea, and W. B. Scott. 1980. A list of common and scientific names of the fishes from the United States and Canada. 4th ed. Am. Fish. Soc. Spec. Publ. No. 12: 174 p.

Robinson, J. W. 1980. Results of wing dike modifications on the Missouri River, p. 97–104. *In* Proc. Annu. Meet. Upper Miss. Conserv. Committee, Rock Island, IL.

Romanowsky, P. 1984. Progress in the development of Louisiana's Lower Mississippi River water quality management program. La. Dept. Environ. Qual., Water Pollut. Ctrl. Div., Baton Rouge, LA. 8 p + figs. and tables.

Roosa, D. M. 1977. Endangered and threatened fish of Iowa. Spec. Report of Preserves Bd. No. 1., Des Moines, IA. 25 p.

Ryckman, Edgeley, Tomlinson and Associates. 1975. Environmental assessment of the Mississippi River and tributaries project, Cairo, Ill. to Venice, La. Vol 1. USACE, Lower Mississippi Valley Div., Vicksburg, MS. 275 p.

Sabol, B. M., L. E. Winfield, and D. G. Toczydlowski. 1984. Investigation of water quality and plankton in selected aquatic habitats on the Lower Mississippi River. Environmental Laboratory, USACE Waterways Exp. Sta., Vicksburg, MS. 80 p.

Sager, D. R. and C. F. Bryan. 1980. Temporal and spatial distribution of phytoplankton in the Lower Atchafalaya River Basin, Louisiana, p. 91–101. *In* L. A. Krumholz, C. F. Bryan and G. E. Hall [ed.], Proc. Warmwater Streams Sym., Allen Press, Lawrence, KA.

Saucier, R. T. 1974. Quaternary geology of the Lower Mississippi Valley. Ark. Archeol. Soc. Publ. Archeol. Res. Serv. No. 6: 26 p.

1981. Current thinking of riverine processes and geologic history as related to human settlement in the southeast. Geol. Sci. Mgmt. 22: 7–18.

Scarpino, P. V. 1985. Great river, an environmental history of the Upper Mississippi, 1890–1950. Univ. Mo. Press, Columbia, MO. 219 p.

Schnick, R. A., J. M. Morton, J. C. Mochalski, and J. T. Bailley. 1982. Mitigation and enhancement techniques for the Upper Mississippi River System and other large river systems. USDI, Fish Wildl. Serv. Res. Publ. 149, Washington, D.C. 714 p.

Schramm, H. L., and C. H. Pennington. 1981. Aquatic habitat studies on the Lower Mississippi River, river mile 480 to 530; Report 6, Larval fish studies — pilot report. Misc. Pap. E-80-1, USACE, Waterways Exp. Sta., Vicksburg, MS.

Schumm, S. A., C. C. Watson, and A. W. Burnett. 1982. Phase I. Investigation of neotectonic activity within the Lower Mississippi Valley Division. Potamology Prog. Report No. 2. USACE, Lower Miss. Valley Div., Vicksburg, MS. 153 p.

Seagle, H. H., Jr., K. S. Lubinski and M. C. Reese. 1980. Phase II, Task I — preliminary sampling and site selection, Pool 26. Report Prep. for Upper Miss. River Basin Comm., Minneapolis, MN.

Simons, D. B., P. F. Lagasse, Y. H. Chen, and S. A. Schumm. 1975. The river environment — a reference document. USDI, FWS, Twin Cities, MN. Contr. No. CER-75-76-DBS-PFL-YHC-SAS-14.

Skrypek, J., and R. Sternberg. 1978. Evaluation of proposed striped bass introduction in Lake Pepin. Staff Report, Minn. Dept. Nat. Resources, St. Paul, MN. 8 p.

Smith, A. B. 1963. Channel sedimentation and dredging problems, Mississippi River and Gulf Coast access channels., Proc. Fed. Interagency Sediment. Conf., Miscell. Publ. No. 970, U. S. Dept. Agricul., U. S. Govt. Printing Off., Washington, D. C.

Smith. P. W. 1979. The fishes of Illinois. Univ. Ill. Press, Urbana, IL. 304 p.

Smith, P. W., A. C. Lopinot, and W. L. Pflieger. 1971. A distributional atlas of Upper Mississippi River fishes. Ill. Nat. Hist. Surv. Biol. Notes No. 73: 1–20.

Soileau, L. D., K. C. Smith, R. Hunter, C. E. Knight, D. M. Soileau, W. E. Shell, Jr., and D. W. Hayne. 1975. Atchafalaya Basin usage study final reports, July 1, 1971 – June 30, 1974. USACE, New Orleans Dist., New Orleans, LA. 85 p.

Southall, P. D. 1982. Paddlefish movement and habitat use in the Upper Mississippi River. M.S. thesis, Ia. State Univ., Ames, IA.

Sparks, R. E. 1984. The role of contaminants in the decline of the Illinois River: Implications for the Upper Mississippi, p. 5–24. *In* J. G. Wiener, R. V. Anderson, and D. R. McConville [ed.]. Contaminants in the Upper Mississippi River. Butterworth Publishers, Stoneham, MA. 384 p.

Sparks, R. E., F. C. Belllrose Jr., F. Paveglio, M. Sandusky, D. Steffeck, and C. Thompson. 1979. Fish and wildlife habitat changes resulting from construction of a nine-foot channel on Pools 24, 25 and 26 of the Mississippi River and the Lower Illinois River. Contr. Rept. to USACE, St. Louis District, St. Louis, MO. 217 p.

Stang, D. L., and J. G. Nickum. 1985. Radiotracking of catfish and buffalo in Pool 13, Upper Mississippi River. Letter Order Report No. NCR-IA-85-0048. USACE, Rock Island District. Rock Island, IL. 44 p.

Stoeckel, J. 1985. Nuclear fish program for Pool 14 of the Upper Mississippi River. *In* Proc. 41st Annu. Upper Miss. River Conserv. Committee, Rock Island, IL.

Strahler, A. N. 1952. Hypsometric (area-altitude) analysis of erosional topography. Bull. Geog. Soc. Am. 63(4): 1117–1142.

Strand, R. F. 1980. The walleye sport fishery in three upper Mississippi reservoir lakes: Cass, Andrusia, and Big Wolf, 1971–75. Minn. Dept. Nat. Resources. Invest. Report No. 368. 38 p.

Strand, R. F., and W. J. Scidmore. 1969. Sonar, an aid to under-ice rough fish seining. Minn. Dept. Conserv. Spec. Publ. No. 68, St. Paul, MN.

Strauser, C. 1987. Environmental engineering. *In* Proc. 42nd. Annu. Meet., Upper Miss. River Conserv. Committee, Rock Island, IL.

Sutton, K. 1986. Arkansas' fragile menagerie — endangered and threatened species in the natural state. Ark. Fish and Game. 17(1): 14-19.

Talbot, M. J. 1982. Catfish wintering habitat evaluation. *In* Mississippi River Work Unit Annu. Report 1981-1982. Wis. Dept. Nat. Resources, LaCrosse, WI.

1984. Evaluation of flathead catfish habitat selection, *In* Miss. River Work Unit Annu. Report 1982-83. Wis. Dept. Nat. Resources, La Crosse, WI. p. 87-103.

Talbot, M. J., and B. Parsons. 1985. Evaluation of change in backwater habitat resulting from water flow introduced into Question Slough and Fountain City Bay, Pool 5A, Mississippi River. *In* Miss. River Work Unit Annu. Report, 1983-84. Wis. Dept. Nat. Resources, La Crosse, WI.

Thompson, J. D. 1969. Feeding behavior of diving ducks on Keokuk Pool, Mississippi River. M.S. thesis, Ia. St. Univ., Ames, IA. 79 p.

1973. Feeding behavior of diving ducks on Keokuk Pool, Mississippi River. J. Wildl. Manage. 37(3): 367-381.

Thorn, W. C. 1984. Effects of continuous fishing on the walleye and sauger populations in Pool 4, Mississippi River. Minn. Dept. Nat. Resources, Div. Fish and Wildl. Invest. Report No. 378. 52 p.

Tiffany L. H., and M. E. Britton. 1971. The algae of Illinois. Hafner, New York, NY. 407 p.

Townsend, C. H. 1902. Statistics of the fisheries of the Mississippi River and tributaries (for the year 1899), p. 659-740. *In* U.S. Comm. Fish. Fisheries Report for 1901, Washington, DC.

Tuttle J. R., and W. Pinner. 1982. Analysis of major parameters affecting the behavior of the Mississippi River. Report 4, Potamology Prog. (P-1). USACE, Lower Miss. Valley Div., Vicksburg., MS. 30 p. + tables.

Underhill, J. C. 1957. The distribution of Minnesota minnows and darters in relation to Pleistocene glaciation. Minn. Mus. Nat. Hist. Occasion. Pap. No. 7. 45 p.

Upper Mississippi River Basin Commission. 1982. Comprehensive Master Plan for the Management of the Upper Mississippi River System. Upper Miss. River Basin Comm., Minneapolis, MN. 193 p. + app.

Upper Mississippi River Conservation Committee. 1982. Outdoor recreation: big business on the Upper Mississippi River System. Upper Miss. River Conserv. Committee Spec. Publ., Rock Island, IL.

1953. - 1985. Annual Proc. Upper Miss. River Conserv. Committee, 1830 2nd Ave., Rock Island, IL.

U.S. Army Corps of Engineers (USACE). 1977. Master plan for public use development and resource management. Miss. River Headwaters Reservoirs. St. Paul Dist., St. Paul, MN.

1982. Upper Miss. River Navigation Charts. USACE. Chicago, IL. 170 charts.

1983. Flood control and navigation maps of the Mississippi River: Cairo, IL to the Gulf of Mexico. 51st. Ed., Miss. Riv. Comm., USACE, Vicksburg, MS., 107 charts.

1985. Upper Mississippi River System Environmental Management Program — General Plan. N. Cent. Div., Chicago, IL. 31 p.

U.S. Dept. Commerce. 1978. Fisheries Statistics of the United States, 1977. NOAA, Nat. Mar. Fish. Serv. 463 p.

1986. Fisheries of the United States, 1985. Current fisheries statistics, No. 8380. Nat. Mar. Fish. Serv., Washington, D.C.

U.S. Fish and Wildlife Service. 1982. 1980 national survey of fishing, hunting and wildlife associated recreation. USDI, U.S. Fish and Wildl. Serv., Washington, D. C. 156 p.

1985. Great Lakes "Red Book" for threatened and endangered species. USDI, FWS, Reg. III., St. Paul, MN.

U. S. Geological Survey. 1983a. Water Resources Data for Minnesota. MN-83-2. U.S. Dept. Int., St. Paul, MN.

1983b. Water Resources Data for Missouri. MO-83-1. U.S. Dept. Int. Jefferson City, MO.

1983c. Water Resources Data for Arkansas. AR-83-1. U.S. Dept. Int. and Ark. Geol. Comm., Little Rock, AR.

Van Vooren, A. 1983. Distribution and relative abundance of Upper Mississippi River fishes. Upper Miss. River Conserv. Committee, Spec. Publ., Rock Island, IL. 20 p.

1984. Population dynamics of Mississippi River largemouth bass. Proj. No. 83-III-P-13, Ia. Conserv. Comm., Des Moines, IA. 34 p.

Waters, S. 1976. Expandable creel survey below Lock and Dam 16, Mississippi River, p. 54-68. *In* 1976 Job Compl. Report, 1977 Mgmt. Plan and Stocking Guidelines. Ia. Conserv. Comm. Proj. No. 76-III-C-15.

Waters, T. F. 1977. The streams and rivers of Minnesota. Univ. Minn. Press, Minneapolis, MN. 373 p.

Watson, L. D., and B. W. Hawkinson. 1979. Recreational use of Pool 5, Mississippi River. Upper Miss. River Conserv. Committee Spec. Publ., Rock Island, IL. 23 p.

Wells, F. C. 1980. Hydrology and water quality of the Lower Mississippi River. Tech. Report No. 21., La. Dept. Trans. and Develop., Off. Pub. Works, Baton Rouge, LA. 83 p. + 5 plates.

Wells, F. C., and C. R. Demas. 1977. Hydrology and water quality of the Atchafalaya River Basin. Tech. Report No. 14. U. S. Fish and Wildl. Serv., La. Dept. Public Works and U. S. Geol. Surv., Baton Rouge, LA. 53 p.

Wiener, J. G., G. A. Jackson, T. W. May, and B. P. Cole. 1984. Longitudinal distribution of trace elements (As, Cd, Cr, Cu, Ni, Pb, Zn) in fishes and sediments in the Upper Mississippi River, p. 119-138. *In* J. G. Wiener, R. V. Anderson, and D. R. McConville [ed.] Contaminants in the Upper Mississippi River. Butterworth Publ., Stoneham, MA.

Wright, H. E., Jr. 1972a. Quaternary history of Minnesota, p 561-578. *In* P. K. Sims, and G. B. Morey [ed.] Geology of Minnesota: a centennial volume. Minn. Geol. Surv., St.Paul, MN.

1972b. Quaternary history of Minnesota, p. 515-547. *In* P. K. Sims, and G. B. Morey [ed.] Geology of Minnesota: a centennial volume. Minn. Geol. Surv., St. Paul, MN.

Wright, K. J. 1970. The 1967-1968 sport fishery survey of the Upper Mississippi River. Upper Miss. River Conserv. Committee Spec. Publ., Rock Island, IL. 116 p.

Zimpfer, S. P., W. E. Kelso, C. F. Bryan, and C. H. Pennington. 1986. Ecological features of eddies associated with revetments in the Lower Mississippi River. USACE Waterways Exp. Station. Vicksburg, MS, Ecol. Rep. No. 8: 62 p.

Zimpfer, S. P., C. F. Bryan, and C. H. Pennington. 1987. Factors associated with the dynamics of grass carp larvae (*Ctenopharyngodon idella*) in the Lower Mississippi River Valley. Am. Fish. Soc., Symp. 2: 102-108.

Missouri River Fishery Resources in Relation to Past, Present, and Future Stresses

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Abstract

HESSE, L.W., J.C. SCHMULBACH, J.M. CARR, K.D. KEENLYNE, D.G. UNKENHOLZ, J.W. ROBINSON, AND G.E. MESTL. 1989. Missouri River fishery resources in relation to past, present, and future stresses, p. 352–371. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Nearly one-third of the Missouri River has been impounded, one-third channelized, and the hydrologic cycle, including temporal flow volume and sediment transport, has been altered on the remainder. The floodplain along the lower one-third has been converted from riparian forest and prairie to agriculture. The changes in basin and floodplain physiography and channel morphology have reduced commercial fish harvest by more than 80 % and are implicated in the demise of native species. In some instances nonnative fish have replaced endemic species in the mainstem reservoirs, where breeding and maturing habitat for riverine species has been eliminated. Suggested solutions include: a holistic approach to future research and management, acquisition of data on minimum flow requirements to maintain or reestablish natural channel morphological features, creation of fish bypass structures around dams on the mainstem and the tributaries, a solution to degradation/aggradation imbalances through mechanical measures to move accumulating sediment from the reservoirs and reestablish lost nutrient and energy cycle pathways, manipulation of reservoir releases to emulate the natural hydrologic cycle, development of structural modifications to recreate lost habitat diversity and contribute to renewed energy cycling, establishment of a moratorium on the stocking of nonnative species of fishes until adequate assessment has been completed, and innovation of means to pay for needed mitigation.

Résumé

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Des ouvrages de retenue ont été érigés sur près du tiers du fleuve Missouri, des chenaux ont été aménagés sur un autre tiers et le cycle hydrologique, y compris l'écoulement dans le temps et le transport des sédiments, a été pertubé dans l'autre tiers. La plaine d'inondation qui longe le tiers inférieur à été transformée, passant d'une forêt et d'une prairie riveraines à une terre agricole. Les changements survenus dans la physiographie du bassin et de la plaine d'inondation et dans la morphologie du chenal ont entraîné une réduction de plus de 80 % des captures commerciales et une diminution des espèces indigènes. Dans certains cas, les poissons non indigènes ont remplacé les espèces endémiques dans les réservoirs de l'axe principal, tandis que l'habitat de reproduction et d'élevage des espèces riveraines a été détruit. Les solutions proposées comprennent: une approche globale à la recherche et à la gestion future, l'acquisition de données sur le débit minimum requis pour maintenir ou rétablir les caractéristiques morphologiques du chenal naturel, la construction d'échelles à poisson pour contourner les barrages érigés sur l'axe principal et les tributaires, une solution mécanique aux déséquilibres entre la dégradation et l'exhaussement afin de déplacer les sédiments accumulés dans les réservoirs et de rétablir les éléments nutritifs perdus et le cycle énergétique, la manipulation des fuites des réservoirs pour stimuler le cycle hydrologique naturel, la modification des structures pour rétablir la diversité des habitats et renouveler le cycle énergétique, l'adoption d'un moratoire sur le peuplement des espèces piscicoles non indigènes jusqu'à ce qu'une évaluation adéquate soit faite, et le financement des ouvrages de réduction.

Introduction

The Missouri River has long served as a travelway and thread of life for humans as well as fish and wildlife. It was a center of trade and cultural exchange long before Captains Lewis and Clark made their historic trip of 1804 to 1806, immediately following the Louisiana Purchase in 1803. Wildlife was abundant then, and the river provided both shelter and water in an otherwise expansive and arid plain.

The Missouri River flows from its confluence with the Gallatin, Madison, and Jefferson rivers in southwestern Montana, near Three Forks, generally east and south to join the Mississippi River just upstream from St. Louis, Missouri (Fig. 1). The Missouri River is 3 768 km in length; six major dams impound 1 233 km of this length; 1 202 km have been channelized; and 1 333 km remains "free flowing" but controlled by reservoir releases. Nearly 95 % of the basin's land mass is devoted to agriculture. Only 1.2 % of the basin is covered by water, but water plays a disproportionately larger role in the economics of the area (U.S. Army Corps of Engineers 1979).

Development of the basin's water resources began in the 1800's in response to the need for a dependable water supply for irrigation, navigation, and mining. Several federal laws

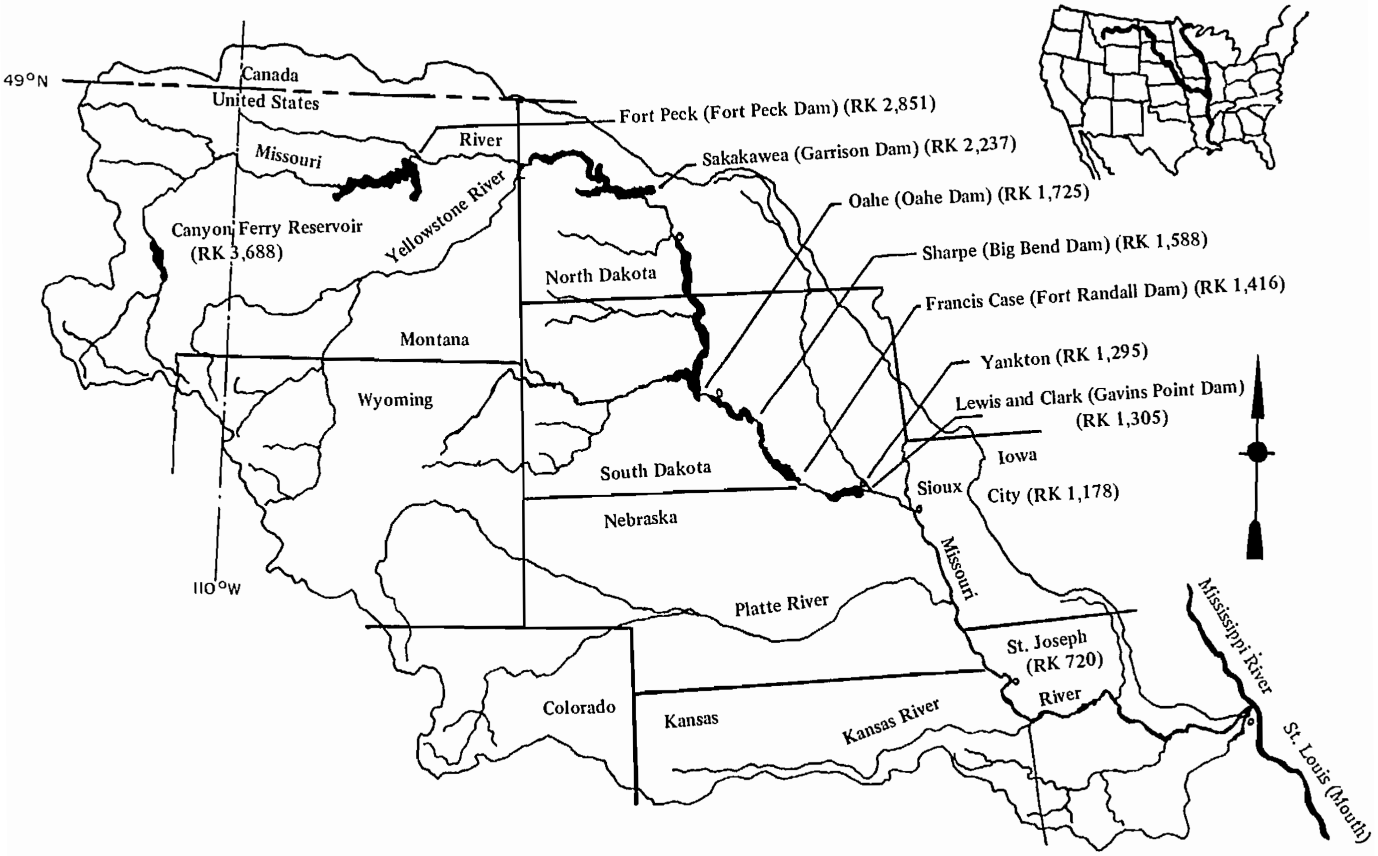

FIG. 1. The Missouri River Basin showing most of the civil works projects that have been completed by the U.S. Army Corps of Engineers, and the U.S. Bureau of Reclamation. Rk represents River kilometre.

impacted these resources. First the Reclamation Act of 1902 fostered irrigation development and settlement of lands in the western United States. Later legislation (1912) created a 1.8 m navigation channel along the Missouri River from the mouth to Kansas City, Missouri. The current dimensions of the navigation channel (2.7 m deep by 91.4 m wide) from the mouth to Sioux City, Iowa were established by legislation enacted in 1945. Lower basin tributary development and levee construction along the mainstem were authorized in 1941. The Pick–Sloan Plan (adopted in 1944) included a comprehensive plan of development for the entire Missouri River Basin. Plan purposes included: irrigation, navigation, hydropower, flood control, water quality, water supply, fish, wildlife, and recreation.

The extensive developments of the Pick–Sloan Missouri Basin Program (P–S MBP) and the river's wildlife resources must one day deal with insufficient water supply as their greatest threat (Lord et al. 1975). By 1970 6.0×10^9 m^3 of water (8.6% of annual discharge) was consumed annually (U.S. Army Corps of Engineers 1979). Evaporation removed nearly 37%, while irrigation accounted for 43% of depletions. Since only 2% of the basin's farmland is under irrigation, this use will contribute most to future additional depletions. Further depletions will intensify reservoir fluctuations, add to peaking power impact, result in an even narrower navigation channel and an altered navigation season, add to the destabilization of aggradation and degradation processes, and complicate water quality maintenance and already untenable fisheries problems.

Since the drainage basin is large with numerous states having jurisdiction over parts of the waterway, no holistic studies from headwater to mouth have been conducted. Consequently, the intent of this paper is to utilize a reprsentative selection of studies to characterize the work which has been done on Missouri River fisheries. Research results will be presented in the context of separate studies on the various river reaches including free-flowing sections and mainstem impoundments. The potential impact of existing and projected threats on the Missouri River fishery resources will be addressed.

Morphometry and Hydrology

The present course of the Missouri river generally outlines the southern extent of Pleistocene glaciation. Prior to Pleistocene glaciation, the river flowed north into Hudson Bay. The advancing ice sheet turned it southward where it gained tributaries, and increased in size. Today the Missouri is the longest river in the United States.

The Missouri River basin encompasses 137 million ha, including 2.5 million ha in Canada. Topography varies from 14.5 million ha of Rocky Mountains in the west, to 95.8 million ha of the Great Plains area in the heartland of the basin, to 23.3 million ha of Central Lowlands in the lower basin. Stream slope varies from about 38 $m \cdot km^{-1}$ in the Rockies to an average 0.17 $m \cdot km^{-1}$ in the Great Plains and Central Lowlands (U.S. Army Corps of Engineers 1985).

South and west of the Missouri River, the surface mantle and topography have been shaped largely by erosion of a fluvial plain extending eastward from the Rocky Mountains. North and east of the Missouri River, and even extending south of the river in some places, the Great Plains have been affected by continental glaciation. Here, the topography was shaped primarily by erosion of the glacial drift and till. This has led to a most prominent feature in the drainage pattern of the upper and middle portions of the basin in that every major tributary, with the exception of the Milk and James Rivers, is a right bank tributary flowing to the east or to the northeast. Only in the extreme lower basin, below the mouth of the Kansas River, is a fair balance reached between left and right bank tributaries (U.S. Army Corps of Engineers 1985).

In the upper portion of the basin, the river runs through canyons and rugged mountain terrain and is a clear mountain stream with a valley only 240 m wide. Upper tributaries which flow through the highly erodable, unglaciated soils, add heavy loads of silt to the river. With the construction of the mainstem dams, the upper end of "Big Muddy" was converted from a heavily silt laden river to a series of deep, cold-water reservoirs. Each reservoir traps the silt loads of tributary streams. In 1944 the river transported 228.6 million t of sediment downstream. By 1954 when the lowermost mainstem dam (Gavins Point) was closed, the average annual silt load was reduced by 81% to 29.5 million t (Slizeski et al. 1982). The silt/clay fraction was reduced 50% while the sand fraction increased 260%.

In the lower basin, before channelization, the Missouri River flood-plain varied from 2.4 to 27.4 km in width and avaraged 8.1 km; present distance from levee to levee ranges from 183 to 335 m. The channelized portion of the Missouri River is now characterized by a single rock-lined channel that is first controlled by regulated releases from the mainstem reservoirs and then contained within high agricultural levees. Remnant portions of unchannelized and unimpounded Missouri River are characterized by eroding banks, braided shifting channels, and sandbars.

The climate of the basin is governed by the interaction of three great air masses originating in the Gulf of Mexico, the northern Pacific Ocean, and the northern polar region (U.S. Army Corps of Engineers 1985). Average annual precipitation varies from over 80 cm in the west (Rocky Mountains) to about 45 cm over the Great Plains, to over 90 cm in the southeast (Ozark Highlands). Nearly 70% of this precipitation falls as rain during the growing season (Missouri River Basin Commission 1980). Average annual discharge to the Mississippi is 7.0×10^{10} m^3. The freeze-free season ranges from less than 40 days (Rocky Mountains) to more than 120 days in the Ozark Highlands.

Prior to reservoir construction the Missouri River experienced two general periods of flooding. The first, often referred to as the "March rise" was caused by snow melt in the plains and the break-up of ice in the mainchannel and tributaries. Heavy precipitation is not always implicated and the crest flattens as it progresses downstream. The upper portion of the river was threatened most by the "March rise" floods (U.S. House Document No. 475 1944). The "June rise" was produced by runoff from melting mountain snow and rainfall throughout the basin. Flooding at this time was most threatening in the lower portion of the basin (U.S. House Document No. 475 1944). The lower Missouri River valley still experiences floods which result from heavy runoff from tributaries downstream of the mainstem reservoirs and/or from ice jams.

The most prominent multipurpose projects on the mainstem are six reservoirs: Fort Peck, Sakakawea, Oahe, Sharpe, Francis Case, and Lewis and Clark (Fig. 1). These reservoirs can store 9.26×10^{10} m^3 of water. Other large storage reservoirs were built on tributary streams by the Corps of Engineers, Bureau of Reclamation, and Bureau of Indian Affairs. The Soil Conservation Service, local districts and private individuals have constructed over 1 300 smaller reservoirs and many more farm ponds all of which serve to control runoff and limit sediment movement (Missouri River Basin Commission 1977).

Since mainstem and tributary reservoirs collect much of the alluvium previously transported downstream, water leaving the dams is capable of transporting a larger sediment load. Between 1929 and 1980, the river's elevation 8.3 km downstream from Gavins Point Dam dropped 2.26 m. Degradation continues to occur at least 346 km downstream to the mouth of the Platte river. Simultaneously, along the river from the Platte–Missouri confluence to the Missouri–Mississippi confluence there has been varying degrees of aggradation resulting in stage rises (U.S. Army Corps of Engineers 1980).

Unnatural degradation/aggradation processes resulted in difficulty in diverting water to intake structures, headcutting in tributary streams, changes in property boundaries and ownership, and deterioration of fish and wildlife habitat (Sayre and Kennedy 1978). Degradation drains major backwaters below each dam. Along the channelized river, oxbow lakes no longer contribute to channel biota but are now perched several meters above the deepening channel bed. Bed armoring would abate degradation, but at best, only small areas show coarse materials near the bed surface. Sediment loading increases from no load at Gavins Point to nearly 86.2 million t annually at the mouth near St. Louis, Missouri. Average suspended sediment concentrations range from 200 to 1500 $mg \cdot L^{-1}$ at normal discharge to 5000 $mg \cdot L^{-1}$ during flooding (Slizeski et al. 1982).

Stage levels follow daily and seasonal changes in discharge and water temperature, bed form, sediment loading, meteorological changes, and localized flow disturbances (Slizeski et al. 1982). For example, discharge rates from August to December stay relatively steady but with seasonal temperature declines the bed form smooths out, flow resistance is correspondingly less, flow velocity increases, and the stage drops.

The difference in storage in the six mainstem reservoirs between the base for flood control and the top is 2.13×10^{10} m^3. Since 80 % of a calendar year's water supply has been received by 1 August, storage is reduced to near the base of flood control in all mainstem reservoirs by 1 March. As spring runoff begins, water is metered out of the three uppermost dams to meet the need for downstream navigation flows, but usually within the powerplant capacities of each dam. This open water release amounts to 700 to 990 $m^3 \cdot s^{-1}$ and lasts from 1 April to 31 November. Daily releases during the non-navigation season (December through March) average between 170 and 650 $m^3 \cdot s^{-1}$ for water quality, power production, and flood control (U.S. Army Corps of Engineers 1985).

Mainstem and tributary dams control water releases for several purposes including power generation, navigation, and flood control. Hydroelectric energy, generated by basin power plants, is marketed by the Western Area Power Administration (WAPA) and the Southwest Power Administration (SPA). During the navigation season, releases from the four uppermost reservoirs are varied to generate the greatest amount of energy at times of greatest power demand. Upstream releases from Fort Peck and Garrison are high in winter, offsetting reduced production from downstream powerplants. During periods of high electrical demand, energy is supplied with the peaking capability at Oahe, Big Bend, and Fort Randall. Figure 2 shows the hydrologic cycle of the Missouri River as it is currently controlled. Gavins Point serves as a re-regulatory dam to even out the often erratic upstream releases and provide uniform flows to the navigation channel.

Downstream commercial navigation and flood control were facilitated by the Missouri River Bank Stabilization and Navigation Project which was completed in 1981. It provided for a controlled river extending 1200 km from Ponca, Nebraska to the confluence wih the Mississippi River. Channel dimensions (2.7 m by 91.4 m) are maintained with dikes, revetments, and sills (Slizeski et al. 1982). Channel hydrodynamics are closely related to the dike system. By design, the channel is nearly self-scouring throughout the 1200 km length. The natural river's "offset V" shape has been transformed into a trapezoidal configuration and channel velocity ranges from 1.5 to 2.1 $m \cdot s^{-1}$ at Omaha, Nebraska when discharge ranges from 849 to 1 981 $m^3 \cdot s^{-1}$ (Slizeski et al. 1982).

Energy Sources and Pathways Toward Fish Production

The proportions and quantities of allochthonous and autochthonous sources of organic matter in the Missouri River is virtually unknow. Little information is currently available quantifying the extent of transfer from one trophic level to the next or of quantities of organic matter imported and exported in any portion of the river.

Except for the headwater reaches the soils of the basin are fine and erodable. Although the reservoirs have reduced turbidity in the river it remains the strongest limiting factor to plankton abundance. Calcium, magnesium, bicarbonates, and sulfates occur in relatively high concentrations and contribute to the high buffering capacity of the water as reflected in stable pH and specific conductance (Benson and Cowell 1968). Minimal industrial pollution exists upstream from Sioux City, Iowa and domestic pollution effects are confined to the areas directly downstream from municipalities (Benson 1968).

Thermal stratification in Fort Peck, Sakakawea, and Oahe occurs in limited areas for part of the summer (Benson 1968). Stratification in Sharpe, Francis Case and Lewis and Clark does not occur due to shallow water, wind, and rapid flushing rate. Summer surface temperatures are 5.6° C colder in Fort Peck and Sakakawea than downstream in Lewis and Clark. In the winter, all six reservoirs develop ice cover. Principal constituents that affect the water quality in the lower river are dissolved and suspended solids, temperature, bacteria (Todd and Bender 1982), and turbidity (Berner 1951). Between Sioux City, Iowa and the mouth, the river has few associated lakes or backwaters and minimal vascular plants as a result of channelization (Berner 1951). The channel structures provide habitat suitable for aufwuchs colonization that partially offsets the loss of natural habitat (Farrell and Tesar 1982).

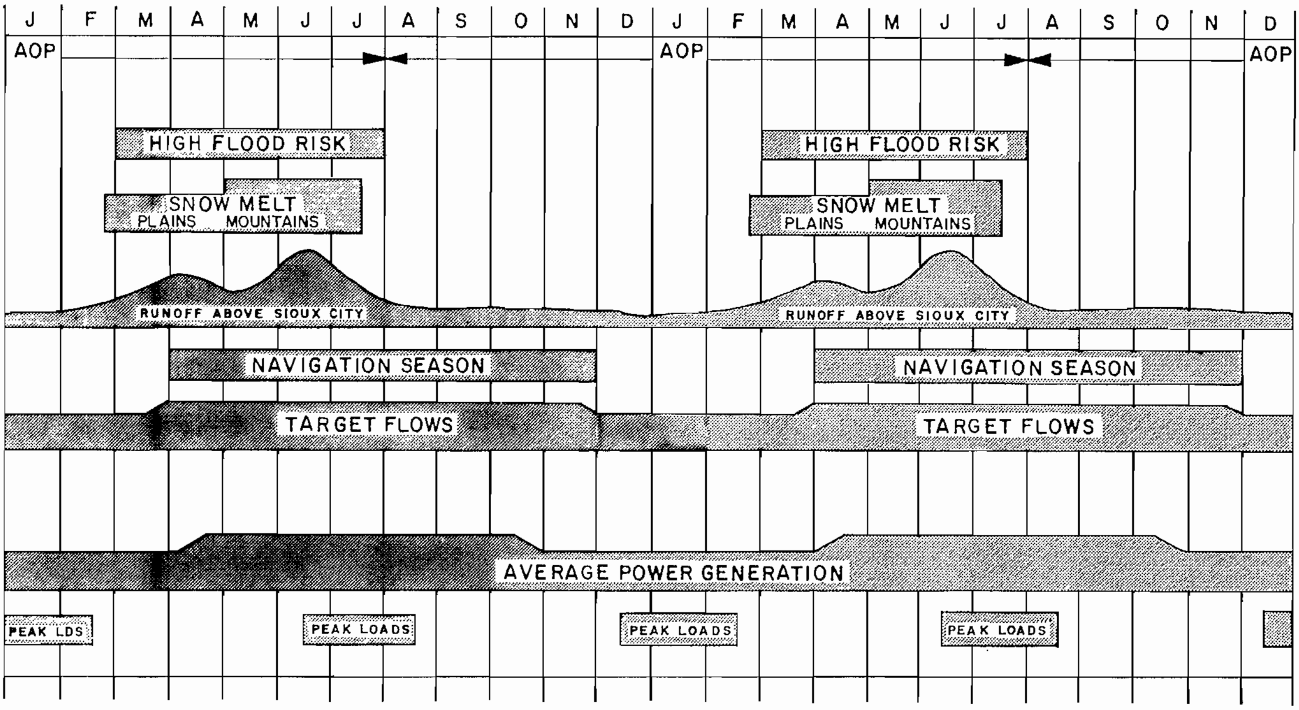

FIG. 2. A calender of water events which describes the Missouri River hydrologic cycle as it is currently controlled (reprinted in part from the 1984 Annual Operating Plant, U.S. Army Corps of Engineers 1985). AOP represents Annual Operating Plan.

Phytoplankton and Periphyton Studies

Diatoms are the most abundant group of the phytoplankton and attached algae in the Missouri River. The mainstem reservoirs downstream from Oahe are increasingly eutrophic, yet net production values are in the range of oligotrophic lakes, with the exception of Lewis and Clark (Martin et al. 1980). Phytoplankton standing crop, primary production, and pigment concentrations progressively increase downstream from Oahe (Damann 1951; Martin et al. 1980). Plankton numbers are reduced in the riverine reaches in direct relation to the length of the river between impoundments (Benson and Cowell 1968; Benson 1968). Comparison of pre— and post-impoundment data showed that phytoplankton numbers were over 10-fold higher after reservoir construction (Benson and Cowell 1968; Benson 1968).

A 1-yr loss of phytoplankton from Lewis and Clark was 9 058 t wet weight, most of which occurred in spring and summer, with nannoplankton composing 84.3 % of the volume (Benson and Cowell 1968). Maximum gross productivity in Lewis and Clark was 1.35 g $C\bullet m^{-2}\bullet d^{-1}$ and 0.74 g $C\bullet m^{-2}\bullet d^{-1}$ in Francis Case (Martin and Novotny 1975). In the lower river, Reetz (1982) found 1 to 25 $\times 10^3$ phytoplankton units per litre from 1974 to 1977 with carbon fixation rates ranging from 45.1 to 154.4 mg $C\bullet m^{-3}\bullet p^{-1}$.

Prior to reservoir construction, periphyton was confined primarily to the tributaries. Substrate availability is limiting in the reservoirs, since most of the reservoir bottoms are a mixture of fine sediments and sand (Benson 1968). In Lewis and Clark, periphytic algal density reached 6 $\times 10^6$ cells$\bullet$ cm^{-2} on submersed trees and water level fluctuations acted to reduce periphyton density (Benson and Cowell 1968). The annual standing crop of periphyton in Francis Case was found to be 100 times less than in Lewis and Clark. Thick growths of *Cladophora* with its associated epiphytic diatoms develop below the dams. Periphyton densities on artificial substrates ranged from 9 $\times 10^5$ to 1.3 $\times 10^7$ units$\bullet$ cm^{-2} (Farrell and Tesar 1982).

Floodplain Vegetation

The most extensive stands of aquatic vascular plants remaining in the Missouri River occur at the confluence of the Niobrara and Missouri rivers, where the Missouri widens and the braided channel contains numerous backwaters. Few data have been collected on the standing crop biomass, dissolved organic matter release, or on periphytic algal communities using them as substrates. The autochthonously produced organic matter input from these stands could be extensive. Aquatic vascular plants are rare in the mainstem reservoirs and have not been studied (Benson 1968).

The natural riparian vegetation of the Missouri River ecosystem has been nearly eliminated (Hesse et al. 1986). Risotto and Turner (1985) found that bottomland hardwood disappearance helped explain the annual variation in the commercial fish harvest of the Mississippi River Basin (including the Missouri River). A decline in the establishment of new trees was attributed to a lack of spring flooding resulting in poor seedbed conditions in North Dakota (Johnson et al. 1976). Soil nutrient content and water retention capacities were greater near older stands because of organic matter buildup. A decline in floodplain forest coverage in the lower Missouri River from 76 % in 1826 to 13 % in 1972 occurred while cultivated land increased from 18 % to 83 % during that time (Bragg and Tatschl 1977).

Zooplankton and Macroinvertebrate Studies

With construction of many reservoirs on the mainstem and the tributaries, zooplankton probably plays a more vital role in trophic relations of many Missouri River fish species. As feeding studies show, though, aquatic insects still fulfill an important link between organic detritus and fish.

Zooplankton standing crops were monitored in the discharge of Francis Case using an automatic plankton sampler from 1966 to 1972; total average monthly zooplankton discharged varied from 43 t in March to 134 t in June (Martin and Novotny 1977). Mean monthly densities of Copepoda and Cladocera were 17 organisms per liter (Cowell 1970). In Lewis and Clark, annual discharge biomass varied from 12 619 to 29 752 t (Benson and Cowell 1968). The amount of plankton entering Lewis and Clark via discharges exceeded the amount discharged from Lewis and Clark (Cowell 1970). However, net loss may not be completely removed from the trophic structure of the reservoir since the dead plankton settling to the bottom may be consumed by benthic invertebrates. A marked increase in populations of *Hexagenia* was found following impoundment of Lewis and Clark and densities were comparable with those in eutrophic bodies of water (Swanson 1967).

Zooplankton numbers are reduced in direct relation with the length of river below Lewis and Clark (Repsys and Rogers 1982). Large initial decreases in reservoir zooplankton are followed by decreasing rates of decline in density downstream. Mean monthly zooplankton densities in the lower river ranged from 7 to 345 organisms per m^3 (Repsys and Rogers 1982).

Variations in morphometry and water management practices are responsible for differences in the benthic invertebrate populations in the reservoirs (Cowell and Hudson 1967). An estimated 44 t (24 t of *Hexagenia* nymphs and 20 t of chironomid and ceratopogonid larvae) were discharged annually from Lewis and Clark (Swanson 1967). Oligochaetes occurred in greatest abundance in the extreme upstream end of that reservoir where organic debris was abundant (Schmulbach and Sandholm 1962). In Oahe the benthos was dominated by oligochaetes and chironomids and estimated at 3 600 organisms per m^2 with an ash-free dry weight of $2.2\ g \cdot m^{-2}$ ($33\ kg \cdot ha^{-1}$ dry weight) (Jones and Selgeby 1974).

Berner (1951) noted that the channelized river current velocity of $0.9 - 3.1\ m \cdot s^{-1}$ and a shifting substratum probably were responsible for the paucity of benthos which, dominated by Chironomidae, averaged less than $7.0\ g \cdot m^{-2}$. Furthermore, these factors were largely responsible for the drift organisms which averaged $1.0\ g \cdot m^{-2}$. Morris et al. (1968) and Nord and Schmulbach (1973) compared the channelized lower river sections with unchannelized river areas. The mean standing crops of benthos were similar but the benthic substrates had been reduced by 67 % in the channelized section. Little similarity was found between the organisms in the drift and the benthos; but drift and aufwuchs organisms were similar.

Increased flow constancy resulted in an enhanced benthic community (Ward 1976) and aufwuchs community (Troelstrup 1985). Numbers of organisms in the drift may increase with both increasing and decreasing discharge (Modde and Schmulbach 1973); it is thus conveivable that short-term flow fluctuations below dams may decimate the fauna even without stranding (Ward 1976). It is recommended that changes in discharge rates should be gradual so that migrating benthos are able to keep up with receding water levels, and drift losses are minimized (Ward 1976)

Food Habits Studies

Food availability and feeding preferences are essential to demonstrate the linkage between detrital components of the Missouri River and the fish community.

Marcroinvertebrates are utilized by most species in the reservoirs except *Stizostedion vitreum*; fish were utilized by *Stizostedion vitreum*, *Stizostedion canadense*, and *Morone chrysops*. *Dorosoma cepedianum* and *Osmerus mordax* were important fish prey for all three species (Unkenholz et al. 1983) while immature *Hexagenia* sp. were an important spring food item (Ruelle 1971). Stomach analysis of *Ictalurus punctatus* in Oahe revealed that the diet was varied with terrestrial insects becoming important during the spring and fall while fish were consumed only in spring (Starostka and Nelson 1974). Zooplankton were a major food item in Francis Case *Ictalurus punctatus* during the summer while filamentous algae were a frequent item in their stomachs during fall. The limited supply of benthic invertebrates in Francis Case, plus the large numbers of terrestrial organisms found in the diet of this species is reflected in their vertical distribution (Unkenholz et al. 1981, 1983). Adult *Ictiobus bubalus* fed primarily on zooplankton and phytoplankton while *Carpiodes carpio* adults consumed mostly organic detritus, zooplankton, and phytoplankton (Walburg and Nelson 1966). Terrestrial and aquatic insects were dominant food items in the annual ration for Lewis and Clark, Oahe, and Francis Case *Hiodon alosoides*. During the summer, zooplankton and Coleoptera were the major food items consumed (Johnson 1963; Miller and Nelson 1974; Unkenholz et al. 1981).

The construction of large reservoirs on the Missouri River has increased the density of zooplankton available. The effects are far reaching and impact feeding behavior even in tailwater reaches.

Food habits studies showed zooplankton were used extensively by young-of-the-year *Ictiobus bubalus*, *Aplodinotus grunniens*, *Pomoxis annularis*, *Morone chrysops*, *Perca flavescens*, *Stizostedion vitreum*, and *Stizostedion canadense* from unchannelized sections downstream from Francis Case and Lewis and Clark (Troelstrup 1985). The abundance of large zooplankters declined during summer in these same tailwater reaches coincident with expanding numbers of age-0 *Dorosoma cepedianum* and *Morone chrysops* (Hesse and Klammer 1984). Michaletz et al. (1987) discovered that zooplanktivorous age-0 fishes in Francis Case selected larger prey as these fish grew. This was especially true for visual predators such as *Stizostedion vitreum* and *Morone chrysops*. In this instance two introduced species of fish are selecting the most abundant and largest zooplankton prey and possibly influencing the seasonal feeding chronology for endemic non-visual predators such as *Ictiobus* spp. and *Polyodon spathula*.

Algae/detritus, phytoplankton, and periphyton are consumed directly by many fish species but, in particular, those inhabiting unchannelized and channelized portions of the river (Berner 1951; Walburg and Nelson 1966; McComish 1967; Nelson et al. 1968; Troelstrup 1985).

Composition of the River Fishery

The fish species known to inhabit the basin streams of which 12 are exotic introductions are listed in Table 1. *Etheostoma nianguae* is considered by the U.S. Fish and Wildlife Service (1986) to be threatened, but 33 other species are listed by basin states as rare, threatened, endangered, or a species of special concern.

The ichthyofauna of a free-flowing reach of river between Great Falls, Montana and the upper end of Fort Peck was extensively studied by Berg (1981). Fifty-three species of fish representing 14 families occur in the Missouri River drainage within this reach, but only 42 species occur in the mainstem. Most species are adapted to cool and warm water. However, in the upstream portion of the river reach between Morony Dam and the confluence of the Marias and Missouri rivers a transition fisheries zone exists where both cold and warm-water species co-exist. *Stizostedion canadense* is the principal game species in this transitional zone but *Salmo* spp. and *Prosopium williamsoni* are also inhabitants. In addition, giant specimens of *Scaphirhynchus platorynchus* inhabit this reach. Upstream from Fort Peck this species averages 767 mm fork length (FL), while downstream they average 561 mm FL (pers. comm. William Gardner, Rod Berg, and Phil Stewart, fisheries biologists with Montana Department of Fish, Wildlife and Parks, Fort Peck, Montana). Temporal instream flow requirements have been established for this extremely unique and important remnant of the Missouri River (Gardner and Berg 1982).

Along this reach *Stizostedion canadense* (68 %) and *Lota lota* (14 %) predominated "game fish only" electrofishing catches (Stewart 1983), while nongame species abundance was very similar to lower Missouri River populations (i.e., *Hiodon alosoides*, *Cyprinus carpio*, *Moxostoma macrolepidotum*, *Carpiodes carpio*, and *Hybopsis gracilis* in decreasing order of abundance).

Stizostedion canadense remains an important game fish in one of the lowermost remnant unchannelized reaches (Niobrara, Nebraska). Electrofishing yielded 5.6 fish per hour (364 mm TL average) in this reach (Hesse and Mestl 1985) compared to 12.8 fish per hour (419 mm TL average) in the reach downstream from Fort Peck (Stewart 1983) which lies five reservoirs and 2800 km upstream.

The portion of Missouri River which was incorporated into the six mainstem reservoirs experienced marked declines in the abundance of species normally distributed in riverine habitats (*Scaphirhynchus platorynchus*, *Scaphirhynchus albus*, *Polyodon spathula*, *Cycleptus elongatus*, *Moxostoma marcrolepidotum*, and *Ictiobus* sp.). In Francis Case, the fish communities were compared over a 23-yr period after impoundment. Of the 39 species collected, 12 were abundant in the 1950's, 8 in the 1970's but only 4 (*Hiodon alosoides*, *Carpiodes carpio*, *Notropis atherinoides*, *Ictalurus punctaus*) throughout the impoundment period (Walburg 1977). *Stizostedion vitreum* and *Morone chrysops* became abundant in the reservoir in the 1970's.

TABLE 1. Fish species of the Missouri River Basin, with distribution by state and present status of the species, and if exotic to the basin (the following literature was used to compile this table: Berard 1985; Brown 1971; Cross 1967; Harlan and Speaker 1956; Jones 1963; Kallemeyn and Novotny 1977; Morris et al. 1974; Personius and Eddy 1955; Pflieger 1975; Pflieger 1971; Robins et al. 1980; Schmulbach et al. 1975; Willock 1969; and Zuerlein 1985).

Species	Distribution and status
Ichthyomyzon castaneus Girard	MO, KS, NE[d]
Ichthyomyzon fossar Richard & Cummins	MO
Ichthyomyzon gagei Hubb & Trautman	MO
Ichthyomyzon unicuspis Hubbs & Trautman	NE, SD, ND
Acipenser fulvescens Rafinesque	MO[b], NE[b], SD
Scaphirhynchus albus (Forbes & Richardson)	MO[b], IA[b], KS[b], NE[b], SD[b], ND[b], MT[b]
Scaphirhynchus platorynchus (Rafinesque)	MO, IA, KS, NE, WY, SD, ND, MT
Polyodon spathula (Walbaum)	MO, IA, KS, NE, SD, ND, MT[b]
Lepisosteus osseus (Linnaeus)	MO, IA, KS, NE, SD, ND
Lepisosteus platostomus Rafinesque	MO, IA, KS, NE, SD, ND, MT[b]
Amia calva Linnaeus	MO, IA, KS, NE, SD
Anguilla rostrata (Lesueur)	MO, IA, KS, NE, SD
Alosa alabamae Jordan & Evermann	MO[b]
Alosa chrysochloris (Rafinesque)	MO, IA[b], KS, NE, SD
Alosa pseudoharengus (Wilson)	NE, SD
Dorosoma cepedianum (Lesueur)	MO, IA, KS, NE, SD
Dorosoma petenense (Gunther)	MO
Hiodon alosoides (Rafinesque)	MO, IA, KS, NE, WY, SD, ND, MT
Hiodon tergisus (Lesueur)	MO, NE
Coregonus artedii Lesuer[d]	MT
Coregonus clupeaformis (Mitchill)	SD, ND, MT
Oncorhynchus kisutch (Walbaum)[d]	NE, SD, ND, MT
Oncorhynchus nerka (Walbaum)[d]	SD, ND, MT
Oncorhynchus tshawytscha (Walbaum)[d]	NE, SD, ND, MT
Prosopium gemmiferum (Synder)[d]	SD, ND
Prosopium williamsoni (Girad)	WY, CA, MT
Salmo aguabonita Jordan	MT
Salmo clarki Richardson	WY, SD, CA, MT[b]
Salmo gairdneri Richardson	MO, KS, NE, WY, SD, ND, CA, MT
Salmo trutta Linnaeus[d]	MO, NE, WY, SD, ND, CA, MT
Salvelinus fontinalis (Mitchill)[d]	NE, WY, CA, MT
Salvelinus namaycush (Walbaum)[d]	SD, ND, MT
Thymallus arcticus (Pallas)	WY, SD, ND, MT[a]
Osmerus mordax (Mitchell)[d]	NE, SD, ND
Esox americanus vermiculatus Lesueur	MO, NE
Esox lucius Linnaeus	MO, IA, KS, NE, SD, ND, CA, MT
Esox masquinongy Mitchill[d]	MO, NE, SD

The rate of change in relative abundance and species composition of reservoir fish has slowed from the first years of impoundment. This is likely a result of the stabilization of habitat in the reservoirs. Annual population changes now reflect success of reproduction, survival of recruits, and

TABLE 1. (cont'd) Fish species of the Missouri River Basin, with distribution by state and present status of the species, and if exotic to the basin (the following literature was used to compile this table: Berard 1985; Brown 1971; Cross 1967; Harlan and Speaker 1956; Jones 1963; Kallemeyn and Novotny 1977; Morris et al. 1974; Personius and Eddy 1955; Pflieger 1975; Pflieger 1971; Robins et al. 1980; Schmulbach et al. 1975; Willock 1969; and Zuerlein 1985).

Campostoma anomalum (Rafinesque)	MO, IA, KS, NE, WY
Campostoma oligolepis Girard	MO
Carassius auratus (Linnaeus)	MO, KS, NE, SD, ND, MT
Couesius plumbeus (Agassiz)	NE, WY, ND[b], CA, MT
Cyprinus carpio Linnaeus	MO, IA, KS, NE, WY, SD, ND, CA, MT
Dionda nubila (Forbes)	MO
Gila atraria (Girard)	MT
Hybognathus hankinsoni Agassiz	MO, IA, KS, NE, WY, SD, ND, CA, MT
Hybognathus nuchalis Hubbs	MO, IA, KS, NE, WY, SD, ND, CA, MT
Hybognathus placitus Girad	MO, KS, NE, WY, SD, ND, MT
Hybopsis aestivalis (Girad)	MO, IA, KS, NE
Hybopsis gelida (Girad)	MO[b], IA, KS, NE, WY, SD[b], ND[b], MT
Hybopsis gracilis (Richardson)	MO, IA, KS, NE, WY, SD, ND, CA, MT
Hybopsis meeki Jordan & Everman	MO[b], IA, KS[b], NE, SD[b], ND[b], MT[b]
Hybopsis storeriana (Kirtland)	MO, IA, KS, NE, SD
Hybopsis x-punctata Hubbs & Crowe	MO
Mylocheilus caurinsu (Richardson)	MT
Nocomis biguttatus (Kirtland)	MO, IA, KS, NE, WY
Notemigonus crysoleucas (Mitchill)	MO, IA, KS, NE, WY, SD, ND, MT
Notropis atherinoides Rafinesque	MO, IA, KS, NE, SD, ND, MT
Notropis blennius (Girad)	MO, IA, KS, NE, WY, SD
Notropis boops Gilbert	MO
Notropis buchanani Meek	MO, KS
Notropis chrysocephalus (Jordan)	MO
Notropis cornutus (Mitchill)	MO, IA, KS, NE, WY
Notropis dorsalis (Agassiz)	MO, IA, KS, NE, WY, SD
Notropis emiliae (Hay)	MO
Notropis greenei Hubbs & Ortenburger	MO
Notropis heterolepis Eigenmann & Eigenmann	MO[b], IA[b], NE
Notropis hudsonius (Clinton)[d]	IA, NE, SD, ND, MT
Notropis lutrensis (Baird & Girard)	MO, IA, KS, NE, WY, SD, ND
Notropis rubellus (Agassiz)	MO, IA, KSS
Notropis shumardi (Girad)	MO, IA, KS, NE, SD
Notropis spilopterus (Cope)	MO, IA, NE, SD
Notropis stilbius (Jordan)	NE
Notropis stramineus (Cope)	MO, IA, KS, NE, WY, SD, ND, MT
Notropis topeka Gilbert	MO, IA[b], KS[b], NE
Notropis umbratilis (Girad)	MO, KS
Notropis volucellus (Cope)	MO
Notropis zonatus (Putnam)	MO
Phenacobius mirabilis (Girad)	MO, IA, KS, NE, WY
Phoxinus eos (Cope)	NE[b], ND[b], CA, MT
Phoxinus erythrogaster (Rafinesque)	MO, KS
Phoxinus neogaeus Cope	NE[b], WY, CA, MT[b]
Pimephales notatus (Rafinesque)	MO, IA, KS, NE
Pimephales promelas Rafinesque	MO, IA, KS, NE, WY, SD, ND, CA, MT
Rhinichthys atratulus (Herman)	IA, NE, SD
Rhinichthys cataractae (Valenciennes)	NE, WY, ND, CA, MT
Richardsonius balteatus (Richardson)	MT
Semotilus atromaculatus (Mitchill)	MO, IA, KS, NE, WY, SD, ND
Semotilus margarita (Cope)	NE[b], WY, ND[b], CA, MT
Ctenopharyngodon idella (Valenciennes)	MO, IA, KS, NE, SD
Carpiodes carpio (Rafinesque)	MO, IA, KS, NE, WY, SD, ND, MT
Carpiodes cyprinus (Lesueur)	MO, IA, KS, NE, WY, SD, ND
Carpiodes velifer (Rafinesque)	MO, IA, KS, NE
Catostomus catostomus (Forster)	NE, WY, ND, CA, MT
Catostomus commersoni (Lacepede)	MO, IA, KS, NE, WY, SD, ND, CA, MT
Catostomas platyrhynchus (Cope)	WY, CA, MT
Cycleptus elongatus (Lesueur)	MO, IA, KS[b], NE, SD, ND[b], MT
Hypentelium nigricans (Lesueur)	MO, IA
Ictiobus bubalus (Rafinesque)	MO, IA, KS, NE, SD, ND, MT
Ictiobus cyprinellus (Valenciennes)	MO, IA, KS, NE, SD, ND, MT
Ictiobus niger (Rafinesque)	MO, IA, KS, NE
Minytrema melanops (Rafinesque)	MO
Moxostoma anisurum (Rafinesque)	MO, IA
Moxostoma carinatum (Cope)	MO, IA
Moxostoma duquesnei (Lesueur)	MO
Moxostoma erythrurum (Rafinesque)	MO, IA, KS, NE, SD
Moxostoma macrolepidotum (Lesueur)	MO, IA, KS, NE, WY, SD, ND, CA, MT
Ictalurus furcatus (Lesueur)	MO, IA, KS, NE, SD
Ictalurus melas (Rafinesque)[d]	MO, IA, KS, NE, WY, SD, ND, MT
Ictalurus natalis (Lesueur)	MO, IA, KS, NE, SD, ND, MT
Ictalurus punctatus (Rafinesque)	MO, IA, KS, NE, WY, SD, ND, CA, MT
Noturus exilis Nelson	MO, IA, KS, CA
Noturus flavus Rafinesque	MO, IA, KS, NE, SD, WY, ND, CA, MT
Noturus gyrinus (Mitchill)	MO, IA, KS, NE, SD, ND
Noturus nocturnus Jordan & Gilbert	MO, KS
Pylodictis olivaris (Rafinesque)	MO, IA, KS, NE, SD
Amblyopsis rosae (Eigenmann)	MO
Typhlichthys subterraneus Girard	MO
Percopsis omiscomaycus (Walbaum)	MO, NE, IA
Lota lota (Linnaeus)	MO[b], KS, NE, WY, SD,

TABLE 1. (cont'd) Fish species of the Missouri River Basin, with distribution by state and present status of the species, and if exotic to the basin (the following literature was used to compile this table: Berard 1985; Brown 1971; Cross 1967; Harlan and Speaker 1956; Jones 1963; Kallemeyn and Novotny 1977; Morris et al. 1974; Personius and Eddy 1955; Pflieger 1975; Pflieger 1971; Robins et al. 1980; Schmulbach et al. 1975; Willock 1969; and Zuerlein 1985).

Lota lota (Linnaeus)	ND, CA, MT
Fundulus catenatus (Storer)	MO
Fundulus diaphanus (Storer)	MO
Fundulus kansae Garman	MO, KS, NE, WY
Fundulus notatus (Rafinesque)	MO, KS
Fundulus olivaceus (Storer)	MO
Fundulus sciadicus Cope	MO, IA, KS, NE, WY
Gambusia affinis (Baird and Girard)	MO, KS
Labidesthes sicculus (Cope)	MO, KS
Culaea inconstans (Kirtland)	IA, NE[b], SD, ND, CA, MT
Morone americana (Gmelin)	NE
Morone chrysops (Rafinesque)[d]	MO, IA, KS, NE, SD, ND
Morone mississippiensis (Jordan & Eigenmann)	IA
Morone saxatilis (Walbaum)[d]	MO, KS, NE, SD
Ambloplites rupestris (Rafinesque)	MO, IA, NE, WY, SD, MT
Archoplites interruptus (Girard)	NE, SD
Lepomis cyanellus Rafinesque	MO, IA, KS, NE, WY, SD, ND, MT
Lepomis gibbosus (Linnaeus)	MO[b], IA, NE, WY, ND, MT
Lepomis gulosus (Cuvier)	MO, IA, KS
Lepomis humulis (Girard)	MO, IA, KS, NE, SD, ND
Lepomis marcrochirus Rafinesque	MO, IA, KS, NE, WY, SD, ND, MT
Lepomis megalotis (Rafinesque)	MO, KS
Micropterus dolomieui Lacepede	MO, IA, KS, NE, WY, SD, ND, MT
Micropterus punctulatus (Rafinesque)	MO, KS, NE
Micropterus salmoides (Lacepede)	MO, IA, KS, NE, WY, SD, ND, MT
Pomoxis annularis Rafinesque	MO, IA, KS, NE, WY, SD, ND, MT
Pomoxis nigromaculatus (Lesueur)	MO, IA, KS, NE, WY, SD, ND, MT
Ammocrypta asprella (Jordan)	MO[b]
Etheostoma blennioides Rafinesque	MO, KS
Etheostoma caeruleum Storer	MO
Etheostoma exile (Girard)	IA, NE, WY, SD, ND, MT
Etheostoma flabellare Rafinesque	MO, KS
Etheostoma gracile (Girard)	MO, NE, SD, ND, MT
Etheostoma microperca Jordan & Gilbert	MO
Etheostoma nianguae Gibert & Meek[c]	MO[b]
Etheostoma nigrum Rafinesque	MO, IA, KS, NE, WY, SD, ND
Etheostoma punctulatum (Agassiz)	MO
Etheostoma spectabile (Agassiz)	MO, KS, NE, WY
Etheostoma tetrazonum (Hubbs & Black)	MO
Etheostoma zonale (Cope)	MO, IA
Perca flavescens (Mitchill)	IA, KS, NE, WY, SD, ND, CA, MT
Percina caprodes (Rafinesque)	MO, IA, KS
Percina cymatotaenia (Gilbert & Meek)	MO[b]
Percina evides (Jordan & Copeland)	MO
Percina maculata (Girard)	MO, IA, KS, NE
Percina phoxocephala (Nelson)	MO, IA, KS
Percina shumardi (Girard)	MO, KS, NE, SD
Stizostedion canadense (Smith)	MO, IA, KS, NE, WY, SD, ND, CA, MT
Stizostedion vitreum vitreum (Mitchill)	MO, IA, KS, NE, WY, SD, ND, CA, MT
Aplodinotus grunniens Rafinesque	MO, IA, KS, NE, SD, ND, CA, MT
Cottus bairdi Girard	MO, CA, MT
Cottus carolinae (Gill)	MO

[a] MO (Missouri); KS (Kansas); NE (Nebraska); SD (South Dakota); ND (North Dakota); IA (Iowa); MT (Montana); WY (Wyoming; CA (California).

[b] Rare, threatened, endagered, or species of special concern.

[c] Listed with U.S. Fish and Wildfile Service as a threatened species.

[d] Exotic introduced into the Missouri River or mainstem reservoirs.

harvest rather than changing habitat. Table 2 provides an index to relative abundance of species by reservoir. Annual gillnet surveys were carried out by bilogists with Montana, North Dakota, and South Dakota fisheries departments.

Introductions of cold-water species into mainstem reservoirs have changed the existing species composition. *Osmerus mordax* has become abundant in Sakakawea and Oahe (Burczynski et al. 1985). Regular stocking of several salmonids has maintained the presence of these species in the upper four reservoirs. *Notropis hudsonius* was introduced successfully into several mainstem reservoirs and is self-sustaining and increasing at the present time.

In the unchannelized river reaches downstream from Francis Case and Lewis and Clark the relative abundance of fishes have been extensively studied. Kallemeyn and Novotny (1977) considered 11 species abundant including *Carpiodes carpio*, *Cyprinus carpio*, *Hiodon alosoides*, *Ictiobus bubalus*, *Ictiobus cyprinellus*, *Ictalurus punctatus*, *Dorosoma cepedianum*, *Moxostoma macrolepidotum*, *Notropis atherinoides*, *Notropis lutrensis*, and *Notropis stramineus*. All are members of the big river faunal assemblage (Pfleiger 1975). Schmulbach et al. (1975) included angling in their collection techniques and listed 14 species as being either abundant or very common in one or more of the six habitat types in the unchannelized river. Included in their list were *Scaphirhynchus platorynchus*, *Lepisosteus platostomus*, *Morone chrysops*, *Stizostedion canadense*, *Aplodinotus grunniens*, *Dorosoma cepedianum*, *Hiodon alosoides*, *Cyprinus carpio*, *Notropis atherinoides*, *Notropis lutrensis*, *Notropis stramineus*, *Carpiodes carpio*, *Moxostoma macrolepidotum*, and *Ictalurus punctatus*.

Channelized river reaches in Nebraska and Iowa have as many species as the unchannelized reach but only six species are abundant: *Cyprinus carpio*, *Carpiodes carpio*, *Hiodon alosoides*, *Ictalurus punctatus*, *Moxostoma macrolepidotum*, and *Ictiobus bubalus*. Collectively these six species constituted 90% of all fish collected by electrofishing over

TABLE 2. Relative abundance of fish in the six mainstem Missouri River reservoirs based upon standard experimental gillnet survey techniques for (catch per gillnet per night) 1984.

Species	Fort Peck	Sakakawea	Oahe	Sharpe	Francis Case	Lewis and Clark
Scaphirhynchus albus		0.1				
Scaphirhynchus platorynchus	0.1		0.1	1.6		
Dorosoma cependianum				1.6	3.9	
Hiodon alosoides	31.1	11.8	2.7	0.4	0.9	
Coregonus clupeaformis		0.1				
Oncorhynchus tshawytscha		0.1	0.1	0.1		
Osmerus mordax		0.1	0.1	0.2		
Esox lucius	1.0	3.5	0.8	0.1	0.1	
Cyprinus carpio	2.2	1.8	2.3	4.3	1.1	0.3
Carpiodes carpio	1.6	0.3	1.3	1.0	0.2	2.1
Catostomus commersoni	0.6	4.6	0.2			
Ictiobus bubalus	0.4	0.1	0.1	0.1	0.1	0.2
Ictiobus cyprinellus		0.1	0.1			
Moxostoma macrolepidotum	4.0	0.9	0.5	0.2		0.2
Ictalurus punctatus		1.0	4.6	4.3	3.2	1.4
Morone chrysops		0.4	1.8	4.0	1.1	1.1
Micropterus dolomieui	0.4	0.1	0.1			
Pomoxis annularis		0.1	0.3	2.2	1.1	0.3
Pomoxis nigromaculatus		0.1				
Perca flavescens	11.0	3.5	19.1	22.1	1.4	
Stizostedion canadense	6.2	18.1	0.3	0.4	0.7	6.4
Stizostedion vitreum vitreum	5.4	10.8	3.8	12.1	14.9	0.4
Aplodinotus grunniens	0.8	1.1	0.6	0.9	1.2	3.4

a 10-yr period (Tondreau et al. 1983). Further downstream in Iowa and Nebraska, the fish community consisted of 57 species but the dominant species were basically the same (Hesse et al. 1982a). The ichthyofauna of the lowermost channelized reach in Missouri reflects the loss of both backwater habitats and in-channel structure such as islands, sandbars and chutes. Here the fish community is dominated by *Cyprinus carpio*, *Ictalurus punctatus*, *Carpiodes carpio*, *Ictiobus bubalus*, and *Ictiobus cyprinellus*, while large specimens of *Ictalurus furcatus*, *Polyodon spathula*, and *Acipenser fulvescens*, have disappeared (Funk and Robinson 1974). Centrarchids which once were abundant in the backwaters are now infrequently collected.

The Missouri River is an open system making population estimates by mark and recapture techniques difficult but several methods have been developed yielding estimates (Table 3) with surprisingly narrow confidence limits. Hesse and Newcomb (1982) estimated that the total population of six species of scaled fish was 2 794• km^{-1}, while *Ictalurus punctatus* populations approached 9 500• km^{-1}. *Scaphirhynchus platorynchus* density estimates were secured from a section of unchannelized Missouri River in 1981 (Schuckman 1982). Despite large variability, mean density was estimated at 966• km^{-1}. Friberg (1974) tagged and released *Polyodon spathula* for 2 yr in the tailwaters of Gavins Point Dam. Fishermen using snagging gear recovered 6 % of the tagged fish and from these returns the population concentrating in the study area was estimated to be 70270 fish. Since no attempt was made to adjust for emigration and immigration this estimate was probably too high (Rosen 1976).

The transformation of the Missouri River into a single channel has resulted in the elimination of most side channels, islands, backwater areas, and sloughs which are important feeding, nursing, resting, and spawning areas for fish and wildlife. Structure modifications including notched, rootless, and low elevation dikes are being used to improve conditions for fish and wildlife in the Missouri River below Gavins Point Dam since 1974. The objective in modifying structures is to stop permanent land accretion and to encourage the river to develop aquatic habitat useable at various river water levels (Burke and Robinson 1979).

Commercial Fisheries

There is very little information available about the early fishery of the Missouri River. Sketchy accounts prior to 1900 spoke of an abundance of very large *Ictalurus* and *Ictiobus*. Funk and Robinson (1974) cited a U.S. Fish Commission report, when in 1894, 143 fishermen reported catching nearly 260000 kg of fish using seines, trammelnets, hoopnets, and trotlines; in 1899, 334 fishermen caught nearly 325 000 kg of fish with similar gear. Jordan and Meek (1885) made several seine hauls in the Missouri River near St. Joseph, Missouri in 1884. From these samples they described 22 species including the following genera: *Lepisosteus*, *Pylodictis*, *Ictalurus*, *Ictiobus*, *Hybognathus*, *Notropis*, *Hybopsis*, *Dorosoma*, *Hiodon*, *Micropterus*, *Lepomis*, *Pomoxis*, *Stizostedion*, and *Aplodinotus*. Fisher (1962) reportedly collected 24 664 specimens in 1945. Many were minnows but of the 7 278 larger fish, the following percentages were observed: *Cyprinus carpio* 35; *Carpiodes* sp. 19; *Ictalurus punctatus*, 9; *Dorosoma cepedianum* 9; *Ictiobus* sp. 6; other Ictalurids 5; *Aplodinotus grunniens* 5; *Hiodon* sp. 4; centrarchids 3; and *Pylodictis olivaris* 2.

The list of commercial fish species is only slightly different between states. This is true as well for licensing requirements, reporting procedures, legal gear, fees charged, and size limit restrictions. The differences, though slight, mandate that interested readers contact individual states for

TABLE 3. Instantaneous numerical density estimates of fish populations in the Missouri River.

	Site by river kilometre	Year	No. .km	Reference
	Channelized river reaches			
Hiodon alosoides	1035	1980	123	Hesse 1983
	1075	1981	1371	Hesse 1983
Cyprinus carpio	1035	1980	1224	Hesse 1983
	1075	1981	607	Hesse 1983
	848	1984	841	Newcomb 1985
Carpiodes carpio	1035	1980	208	Hesse 1983
	1075	1981	1275	Hesse 1983
Ictalurus punctatus	1075	1981	9369	Hesse 1983
	962	1984	529	Newcomb 1985
	1115	1982	1424	Hesse 1983
Pylodictis olivaris	1152	1981	387	Tondreau 1982
	1152	1982	566	Tondreau 1982
	893	1965	16	Morris 1966
Aplodinotus grunniens	1035	1980	240	Hesse 1983
	1075	1981	1371	Hesse 1983
	962	1984	1317	Newcomb 1985
	848	1984	1649	Newcomb 1985
	Unchannelized river reaches			
Scaphirhynchus platorynchus	1272	1981	966	Schuckman 1982
Polyodon spathula	1303	1972	70270	Friberg 1974
Ictalurus punctatus	1287	1976	1015	Hesse 1983

TABLE 4. Commercial harvest (kg) of seven groups of fish by Missouri River border states during 1983.

Location	*Ictiobus* spp.	*Cyprinus carpio*	*Carpiodes carpio*	*Ictalurus* spp.	*Hiodon alosoides*	*Aplodinotus grunniens*	Other	Reference
Kansas	1 657	4 875	1 070	4 575	—	503	185	Stephen 1984
Missouri	40 134	53 543	14 021	56 530	—	13 156	13 397	Robinson 1985
Iowa	24 044	7 347	2 980	2 237	—	443	505	Anon. a. 1983
Nebraska	22 197	32 444	—	20 229	—	—	6 675	Zuerlein 1985
South Dakota[d]	694	—	—	707	—	—	—	Anon b. 1983
North Dakota[b]	43 067	—	—	144	35	1 019	—	Berard 1985
Montana[c]	50 605	2 297	852	—	183 247	41	—	Wiedenheft 1984
Tot. harvest (kg)	182 393	100 501	18 925	84 103	183 282	15 162	20 762	
Value (Dollars)	0.93/kg	0.42/kg	0.42/kg	2.73/kg	1.39/kg	0.82/kg	0.44/kg	

Grand total weight (kg)	605 128
Dollar value	725,716.00

[a] Francis Case (South Dakota enacted (1984) a 5-yr moratorium on commercial fishing in the reservoirs. The Francis Case contract will expire in 1987).
[b] Sakakawea.
[c] Fort Peck.

specific regulations.

The total commercial harvest reported from all states for 1983 was 605 128 kg (Table 4). The monetary value of this catch is over 725 thousand dollars (American Fisheries Society 1982). The reported commercial catch in Missouri has declined steadily from 671 217 kg in 1945 to a low of 70 768 kg in 1965 (Funk and Robinson 1974), and is attributed to lost habitat diversity. The species composition of reported commercial catches has changed little since 1894 (Funk and Robinson 1974) with the exception of *Acipenser* spp., *Polyodon spathula, and Ictalurus furcatus* which have steadily declined, and *Pylodictis olivaris* which is apparently giving way to *Ictalurus punctatus*. It was estimated more recently (Schainost 1981; Hesse et al. 1982b) that total mortality of *Ictalurus punctatus*, over 4 yr old, exceeded 60%. Hesse (1982) estimated that fishing mortality for *Ictalurus punctatus* over 400 mm in total length (6 yr old or older) approaches 100%.

Channelization has played an important role in the ability for commercial fishermen to overharvest a fish resource in a river of this size. Robinson (1985) noted that as the degree of channelization in the Missouri River increased commercial harvest declined below those reported from the Mississippi River. In the late 1940's, when habitats were similar, the harvest in the Missouri River exceeded that from the Mississippi River. Fish are subjected to increased exploitation because the diverse natural aquatic habitat has been compressed into a narrow channel, and because of lost primary and secondary productivity associated with the control over channel meandering and flooding.

The early years of impoundment created conditions favorable for the expansion of many species, followed by a decline in the abundance of several of these. These population changes are reflected in the reservoir commercial harvest. For example 3.5 million kg of 12 species of fish were harvested from Sakakawea, between 1959 and 1984 (pers. comm. Emil Berard, biologist, North Dakota Department of Game and Fish, Riverdale, North Dakota). *Ictiobus* spp. accounted for 41 % of the fish harvested. Garrison Dam was closed in 1953, creating Sakakawea, and the recorded harvest of *Ictiobus* spp. was the lowest at 13 531 kg in 1959. Harvest peaked at 89 793 kg in 1971. Over the first 25 yr of reservoir existence (1959 to 1984), *Ictiobus* spp. harvest has varied considerably. However, since 1977 harvest has averaged 42 283 kg; average for the previous 17 yr was 57 722 kg. Berard attributes some of these changes to increased effectiveness of commercial fishermen (e.g., replacement of gillnets by seines), but a reduction in *Ictiobus* spp. abundance also contributed to the harvest variability. Commercial fishing in the mainstem reservoirs is done primarily to limit competition between commercial and sport fish species (Warnick 1977).

Reservoir Sport Fisheries

Beginning in the 1960's biologists were able to document the aging process of the new reservoirs and resultant changes in fish populations (Benson 1968, 1980; Walburg 1976, 1977). The expanding fish populations which resulted from inundation of terrestrial vegetation were replaced by more stable populations represented by different species. Fish species requiring embayments, brush, or flooded vegetation for spawning decreased in abundance, while species that required less specific habitats or utilized rocky shores, increased (Table 5).

TABLE 5. Abundance and population trend for selected species from Francis Case, 1954 - 1975 (developed from Walburg 1977).

Species	Abundance[a]	Population trend[b]
Scaphirhynchus platorychus	C	D
Polyodon spathula	C	D
Hiodon alosoides	A	I
Cyprinus carpio	C	D
Notropis atherinoides	A	N
Ictiobus cyprinellus	C	D
Ictalurus punctatus	A	I
Morone chrysops[c]	A–C	I
Pomoxis annularis	C	D
Stizostedion canadense	C	D
Stizostedion vitreum	A	I
Aplodinotus grunniens	C	N

[a] A — abundant; C — common.
[b] I — increasing; D — decreasing; N — no trend.
[c] Introduced 1959 to 1961.

Deep, cold pelagic areas created by impoundments provided a unique habitat not utilized by indigenous species. Fish not native to the Missouri River were stocked as well as indigenous species that exhibited low reproductive success (Table 6). Maintenance type stockings were planned for species that did not or could not reproduce successfully in the reservoir situation, (e.g., *Oncorhynchus tshawytscha*). Supplemental stockings of such fishes as *Esox lucius* were done where success of reproduction was variable and managers wished to augment a population that had successive weak year-classes.

Certain introductions required a minimal stocking effort to become established. *Osmerus mordax* was introduced by North Dakota in 1971 (Berard 1985) and were found throughout all mainstem reservoirs downstream from North Dakota by 1976. *Notropis hudsonius* was introduced in Oahe from 1973 to 1975 (Hanten and Talsma 1984) and became established within several years. Table 6 is a summary of stockings made since 1940 into the reservoirs and river segments.

Two crustaceans, opossum shrimp, *Mysis relicta* and an amphipod, *Pontoporeia hayi* were introduced as forage but survival has not been verified. *Mysis* was introduced in Oahe in 1972 to 1974 (Hanten and Talsma 1984) and in Sakakawea in 1973 to 1974 and 1979 (Berard 1985). *Pontoporeia* was introduced into Sakakawea in 1979 (Berard 1985).

Reservoir level manipulation is a useful fishery management tool when conditions allow. States in concert or independently have provided recommendations to the U.S. Army Corps of Engineers (COE) annually. Consideration is given to water yield in the system, existing reservoir water levels, tailwater needs, available shoreline vegetation, availability of spawning habitat relative to reservoir and river level, recent reproductive success, timing of spring runoff, and planned development projects. Tradeoffs must occur. A reservoir may be programmed to hold water at the expense of dropping water levels in another. Given the present management priorities established by the COE, water management within the reservoirs for fish and wildlife occurs only when interference with other purposes does not exist. Water releases from the lowermost reservoir for fish and wildlife management along unchannelized remnants and the entire channelized portion has never been carried out as recommended by state resource managers.

Erosion control and sedimentation are also critical factors in reservoir management since it is estimated that 95 % of reservoir shoreline undergoes active erosion. Watershed erosion control (low head dams, sub-impoundments, grassed waterways, and fencing) has been used or considered as a means to reduce sedimentation of the reservoirs. The importance of this sediment and its included organic material to downstream reaches is unknown, but these reservoirs have probably interrupted carbon cycling.

Little submergent and emergent aquatic vegetation exists due to wind action and water-level fluctuation. Practices such as shoreline seeding, interseeding, hand planting, and fencing have been used (Hoffman 1978) to enhance reproduction of littoral spawners, but have been mostly ineffective. In-lake structures have been constructed in isolated areas where habitat is lacking, submerged vegetation does not exist, or where concentrating fish may enhance success of sport fishing. Examples of structures utilized are: brush shelters, tire reefs, fishing piers, break waters, bank protection and in-lake rock piles. Habitat manipulation also involves reviewing development plans, preparing environmental assessments, acquiring land parcels and easements, and securing water rights. State fish and wildlife agencies have allocated manpower to deal with development and contribute to the assessment of proposed action. Minimizing impacts of proposed actions is one strategy for Missouri River fisheries management.

TABLE 6. Number of fish (by species) stocked into the Missouri River at various locations during the period 1940 to the present (multiply number by 1000).

	Fort Peck	River in Montana	Sakakawea	River in North Dakota	Oahe	Sharpe	Francis Case	River in Nebraska	Lewis and Clark	Total
Polyodon spathula			27		88		291			406
Coregonus artedii	20 050			470						20 520
Coregonus clupeaformis			1		5 300					5 300
Oncorhynchus kisutch	564			1 522	552		10			2 649
Oncorhynchus nerka	387					1 995				2 382
Oncorhynchus tshawytscha	45	262	3 488	929	2 669		607			8 000
Prosopium gemmiferum					84					84
Salmo clarki						165		110		275
Salmo gairdneri	977	89	925	1 035	1 445	1 059	277	20		7 386
Salmo trutta	48		5	51	200	344	25			673
Salvelinus namaycush	474		534		1 395					2 403
Osmerus mordax			7							7
Esox lucius	6 603	9	37 693	100	15 406	1 300	4 869	905	2 400	69 285
Esox masquinongy								72		72
E. lucius/masquinongy						85	25			110
Notropis hudsonius	217		55		17	5	2		53	349
Ictalurus furcatus								1 119	50	1 169
Ictalurus melas	54						4			58
Morone chrysops									7	7
Morone saxatilis									843	843
Lepomis macrochirus	55									55
Micropterus dolomieui	334				666	265	103	89		1 457
Micropterus salmoides	48	1				40	110		75	274
Pomoxis nigromaculatus	165						9			174
Perca flavescens									2	2
Stizostedion canadense	34 427	60	35 336	8	45 593	5	320	2 381	4 952	123 082
Stizostedion vitreum	64 449	421	79 593	2 675	75 555	4 610	6 642	4 696	8 382	247 023

Sport Fishery Harvest and Fishing Pressure

The sport harvest in Francis Case is a good example of the pattern of change which occurred as a result of impoundment. In 1954, while the reservoir was still filling, angling pressure was low, amounting to 84 000 h or 4.1 h• ha^{-1}. Expanding populations of several centrarchids and *Esox lucius* resulting from newly inundated vegetation, more available nutrients, and an expanding environment produced a high rate of angling success (1.37 fish• h^{-1}). At that time less than 0.1 % of all fish creeled were *Stizostedion vitreum*. By 1960 annual angling pressure increased to 425 000 h or 11.7 h• ha^{-1}, approximately its present level, but the harvest rate declined to 0.27 fish• h^{-1}. *Stizostedion vitreum* comprised about 1 % of the harvest. After the normal water management regimen had been in place for several years, plant substrate spawners were unable to maintain large populations. Inundated vegetation decayed and the shoreline eroded to primarily a gravel, rock, mud substrate favoring *Stizostedion vitreum*. In 1984 this species constitued 93.6 % of all fish harvested (Stone 1985a).

Since the advent of the mainstem dams extensive sport fisheries have developed in their tailwaters. The annual fishing pressure in the tailwater of Gavins Point Dam often exceeds 1100 h• km^{-1} (Table 7). Much of the late fall through early spring sport fishing pressure here was the result of a highly successful snagging fishery for *Polyodon*. In very recent years *Polyodon* density and average size and age has declined dramatically. Harvest is now severely restricted.

Groen and Schmulbach (1978) found the annual fishing pressure rates in the unchannelized river downstream of Gavins Point Dam were approximately half (11.5 h• ha^{-1}) that in 412 km of channelized river (21.6 h• ha^{-1} despite harvest rates that were twice as high. The channelized river reach is closer to a population center (Omaha) and most anglers in this study (75 %) lived within 32 km of the river. Lack of good public access to the river contributes to low angler useage in free-flowing reaches (Groen and Schmulbach 1978; Hesse 1979).

Fishing pressure rates in the three lowermost reservoirs on the mainstem vary between 10.9 and 17.1 h• ha^{-1}, which constitutes 40–60 % of the 27.8 h• ha^{-1} observed in seven pools of the upper Mississippi River (Wright 1970).

Sport Fishing Regulations

Sport fishing regulations are the responsibility of the states and are aimed at controlling the fishermen with little relationship to the biological health of the fish community. Special regulations for the Missouri River fishery have existed for only about 30 yr. In recent times states sharing a common boundary have adopted similar regulations, but many differences still exist.

All states permit the collection of fish with hook and line, bow and arrow, spears or gigs, trotlines or other types of set or floating lines, seines for bait fish, and in a few cases hoopnets. Creel limits vary considerably depending upon the relative abundance of the species in a river reach and

TABLE 7. Estimates of fishing pressure, catch, and harvest of the sport fishery in various Missouri River reaches.

	Harvest			Pressure	Rate	
	No.	No. • h	kg• h	h	h• ha	Reference
Oahe, SD						
	342 682	0.27		1 276 990	14.0	Riis 1983
	141 476	0.18		784 658	8.6	Riis 1985
Sharpe, SD						
	113 800	0.33		340 131	15.2	Schmidt 1975
	87 033	0.32		268 425	12.0	Riis 1986
	128 849	0.42		309 373	13.9	Riis 1986
Francis Case, SD						
	115 000	1.37	0.17	84 010	4.1	Shields 1955
	105 000		0.88	119 000		Shields 1956
	114 310	0.27	0.11	425 000	11.7	Nelson 1961
	173 730			565 893		Miller 1984
	136 150	0.24	0.16	557 576	12.9	Miller 1984
	102 073	0.24	0.16	425 059	11.1	Unkenholz et al. 1984
	259 070	0.60		433 636	11.2	Stone 1985a
Fort Randall tailwaters, SD						
	16 615	0.40		41 499		Stone 1985b
Unchannelized river, SD (downriver from Fort Randall Dam)						
	8 724	0.21		40 888		Stone 1985b
Lewis and Clark, NE						
	7 569	0.38		19 874	1.5	Stone 1985b
Gavins Point tailwaters, NE						
	17 112	0.33	1.92	135 545	434.3	Groen and Schmulbach 1978
	22 702	0.21		108 103	1 108.7	Hesse 1979
	45 101	0.57		79 743		Stone 1985b
Unchannelized river NE						
	31 679	0.50	0.87	63 357	11.5	Groen and Schmulbach 1978
Channelized river, NE						
	55 577	0.26	0.40	213 758	21.6	Groen and Schmulbach 1978
	21 385	0.20	0.09	106 478	14.2	Hesse 1979
	Snagging fishery for *Polyodon spathula*					
Unchannelized river, MT						
	664	0.08	2.02	8 299		Berg 1981
Gavins Point tailwaters, NE						
	4 192	0.32	2.51	13 202	42.3	Groen and Schmulbach 1978
	2 274	0.13	0.52	17 492	179.4	Stone 1985b

its popularity with anglers. *Ictalurus punctatus*, for example, are not actively sought by anglers from North Dakota and Montana and neither state has a creel limit on this species. The daily creel limits on *Stizostedion vitreum* and *Stizostedion canadense* range from 4 in Missouri to 10 in Iowa and Montana.

Several states have minimum total length limits of 76 cm on Esocids. Missouri also has adopted a 51 cm minimum size limit on *Morone saxatilis* or *Morone saxatilis*/*Morone chrysops* hydbrids. Montana has established a maximum weight limit of 7.3 kg, while North Dakota has a maximum total length limit of 91 cm for *Scaphirhynchus* spp. These limits were designed to protect the larger *Scaphirhynchus albus* which is severly reduced in number and difficult for most anglers to identify.

Protected Species

Impoundment, channelization, and subsequent water control has no doubt eliminated uncounted species of aquatic life. This loss will continue and it is best expressed in the state by state listings of threatened fish species (Table 1). Agencies in every state in the Missouri River drainage have established a list of fish whose populations in their state are small or declining and worthy of protection (Houtcooper et al. 1985; Lock 1977; McKenna and Seabloom 1979; Missouri Department of Conservation 1984; Roosa 1977). Many species are found primarily in smaller tributary streams, which to some degree are channelized and/or dammed.

Most states have followed the federal system of classifying fish, using the endangered, threatened and rare categories to express different degrees of concern for the species in their state. States on the periphery of a species range may list a species as being rare within their boundaries while the fish is abundant in another state. For example, *Lepisosteus platostomus* in Montana is a species of special concern while in most of the other states it is abundant. Similarly *Cycleptus elongatus* is a threatened species in Kansas and North Dakota but not in the other states. *Acipenser fulvescens* and *Ichthyomyzon castaneus* were probably never abundant in the Missouri River. However, *Scaphirhynchus albus* is listed by every state in the drainage as either endangered, threatened or of special concern (Table 1). Two cyprinids, *Hybopsis meeki* and *Hybopsis gelida* are listed as either endangered, rare or threatened by four and five states, respectively. Perhpas *Polyodon spathula* is the most interesting fish because they appear on the Montana species of special concern list, yet they are legal game fish in Montana as well as in all states in the Missouri River drainage. Only *Etheostoma nianguae* of the species listed in Table 1 is currently on the U.S. Department of Interior's official list of endangered and threatened species (U.S. Fish and Wildlife Service 1986). However, both *Acipenser fulvescens* and *Scaphirhynchus albus* are candidates for inclusion on the federal list (Houtcooper et al. 1985).

Recently *Sterna albifrons* (least tern) has been listed as endangered by the U.S. Fish and Wildlife Service. This is an important development since effort taken to protect this bird may impact fish management programs.

Mitigation Planning

Mitigation planning can be construed as the most potentially significant management practice since habitat alteration took place, but mitigation has not been accomplished. By 1965 all mainstem dams were closed and filling; 462 895 ha were inundated and 1 215 km of river was turned into reservoir (U.S. Army Corps of Engineers 1985). In the northern plains former bottomlands afforded the only real diversity of habitat for terrestrial animals; and the value of the river itself as a home for fish, furbearers, and waterfowl can only be surmised.

Along the lower portion of the river, channelization resulted in construction losses of 41 000 ha of aquatic habitat and 152 000 ha of terrestrial habitat. Accreted and protected floodplain lands are now largely agricultural and are of no value to fish and low value to wildlife. Eventual levee construction, land use changes, and development along the controlled channel has and will continue to deteriorate remaining aquatic and terrestrial habitat. The U.S. Fish and Wildlife Service (1980) estimated that land use changes have impacted fish and wildlife resources on 728 460 ha of the floodplain. As discussed in other sections there are significant environmental problems associated with much of the remaining unchannelized, unimpounded river portions.

Five mitigation proposals have been explored since construction of the P–S MBP started. Only one of these plans has been approved, however, none have been funded. More than 6 billion dollars have been spent to develop water resources and almost no money has been spent to mitigate lost natural resources (Hesse 1987). The Missouri River basin exemplifies the failure of mitigation policy.

National Protection of River Reaches

Subsequent to the passage of national legislation to protect wild and scenic rivers in 1968, two reaches of the Missouri River have been accorded protection; a 93 km reach downstream from the last mainstem dam which was designated a recreational river, and a 240 km section in Montana which received a wild and scenic designation.

Recreational River Section

The Recreational Missouri River corridor is located in the eastern portions of the states of Nebraska and South Dakota where it forms their common boundary. It extends downstream from the tailwaters of Gavins Point Dam at river km 1 303 to the downstream side of Ponca State Park (Nebraska) at river km 1 210. The river channel remains essentially in a natural condition although the water releases are regulated through Gavins Point Dam and the sediment free water leaving Gavins Point has caused severe channel degradation (U.S. Department of Interior 1979).

In the late 1960's and early 1970's an effort was made to extend the navigable channel from Sioux City, Iowa to Yankton, South Dakota near Gavins Point Dam. This attempt was countered by environmental groups and eventually channelization plans were discarded and only a solution to high-bank erosion was pursued since high-bank erosion was of concern to local riparian landowners. High-bank stabilization proceeded slowly at first adressing only the most immediate problem areas but destruction of existing floodplain and riverine habitats continued as did the severe erosion. The 93 km segment of the Missouri River was finally designated a National Recreational River project in 1978. The project is unique since it combines high-bank stabilization structures with the development and operations of recreational and wildlife management areas. Unquestionably the desires of riparian landowners for high-bank stabilization structures provided the principal motivation for a political solution utilizing federal legislation as a vehicle to accomplish this goal. Presently, the project is undergoing review with respect to spending authority, since the question has been raised that local cost-sharing should have been included.

Wild and Scenic Section

A 240 km free-flowing segment of Missouri River extending from Morony Dam near Great Falls, Montana to the Robinson Bridge near the headwaters of Fort Peck was incorporated into the National Wild and Scenic River network in 1976. This reach possesses extraordinary historical, recreational, scenic, and natural values. Inclusion into the national system accords the river protection form federal dam or stream-channel projects and imposes regulations on new commercial development in the designated area adjacent to the protected waters (Berg 1981). A management plan was drafted in 1978 which included as one of its main objectives the determination of instream flow rates needed to maintain existing aquatic communities, recreational opportunities, and water quality parameters commensurate with the purposes of the act. The temporal maintenance of minimum instream flows has the greatest potential of any management practice in maintaining the Missouri River fishery resource at its present level.

Conclusions and Recommendations

The Missouri River drains 137 million ha as it courses 3 768 km from the Rocky Mountains to its confluence with the Mississippi River and traverses through highly erodable, semiarid land under the jurisdiction of seven sovereign states. Human needs and desires to use the water and control the river eventually led to extensive development of the mainstem, tributaries, and riparian floodplain. Currently two-thirds of the mainstem is severely altered by impoundment and channelization. Actually only 40 km at the river's source is free of man's influence. Even if no additional water development were to occur, which is unlikely, it may take decades before the abiotic and biotic components of this complex ecosystem reach a state of dynamic equilibrium. The natural river functioned as an integrated system. Perhaps the greatest cost of changing the face of the river has been the interuption of energy flow into the system from allochthonous sources.

The Pick–Sloan Missouri Basin Program (P–S MBP) (embodying more than 100 major water development projects) has had the most profound influence in the basin. The backbone of this plan is the six mainstem reservoirs in the middle Missouri River reach. The reservoirs were designed to produce multiple benefits including flood control, hydroelectric power, irrigation, navigation, municipal water supply, water quality, recreation, and fish and wildlife. Since federal projects are intended to benefit the public, multiple objectives are nominally attributed to most projects and specified in the enabling legislation. However, the priorities for water useage are not mandated by law but established by the managing federal agencies, while fisheries and related interests are state responsibilities.

State agencies charged with fishery management have no control over water management and can only recommend a plan for temporal discharge. Moreover, states often disagree about water management practices, since each is concerned about the fishery in their respective state. As a consequence fishery managers have never spoken with a single voice and fisheries management has been given a low priority by federal agencies controlling water useage. No integrated holistic plan for either the study or the management of Missouri River aquatic communities has ever been attempted.

We believe that new approaches will be necessary to solve some of the vexing problems. Shifts in priorities will be necessary and all water management changes will be opposed by other interests equally zealous in championing their causes. Nevertheless, a holistic approach to managing the Missouri River ecosystem is the best way to preserve and perhaps even augment habitat diversity and the fishery resources.

Specifically we suggest that some of our management problems could be solved by adopting the following recommendations:

1) Create an organization which coordinates research and management efforts in the entire Missouri River basin. This organization should be dominated by biologists actively managing or researching the resource. All states in the watershed (not just those adjacent to the mainstem) should be represented as well as U.S. Fish and Wildlife Service biologists.

2) Controlled release of water is one tool available to fisheries managers. However, before recommending water releases we need basic information concerning flow requirements for aquatic communitities including the temporal timing, length, and frequencies of the releases. Montana has taken the lead in this area as they established temporal instream flow requirements in the Wild and Scenic reach of the Missouri River. Their study approach was to determine minimum flow rates necessary to maintain channel morphlogy (dominant discharge rates) as well as provide sufficient water for fish and invertebrate communities. The timing, length, and frequency of occurrence of the critical water releases were also determined. These types of studies are also needed for other free-flowing reaches if we are to maintain and enhance ecosystem habitat diversity. Determining flow requirements will be easier than getting them incorporated into an operational plan because the ultimate decision will be predicated on politics.

3) Missouri River fisheries management on a systemwide basis mandates that fish must have unencumbered access to all reaches of the river. Most riverine or lotic-adapted species exhibited extensive movement between reproductive, rearing, and wintering sites. This is especially true for *Polyodon spathula* and *Acipenser* spp. All mainstem dams need a fish bypass to effectively allow passage, an expensive but structurally feasible solution.

4) We must immediately address the problem of channel bed degradation in the free-flowing river reaches below the mainstem dams. The channel bed in free-flowing areas has deepened several meters which eliminated many of the backwater and subsidiary channels. Those habitat types must be preserved because we believe much of the river's autochthonous primary and secondary production occurs in these habitats. Their loss has had a major impact on the flow of energy to the higher trophic levels.

The solution to degradation may even contribute to the solution of other problems. For example, each reservoir has a predicted storage life based upon calculated depositional rates. If entrapped sediment could be moved via side channels from the reservoir around the dam into the free-flowing reaches downstream, the storage life of a reservoir could be extended. More importantly it could add to the sediment load being carried by the river downstream from the dams. This could significantly reduce the amount of degradation in the free-flowing reaches and contribute organic matter to downstream habitats. These sediment channels may also serve as the needed fish bypass.

5) Another proposal that needs exploration is controlled flooding, as a means to maintain habitat diversity. This proposal appears on face value to be diametrically opposed to the principal objective of the Pick–Sloan plan, viz. control flooding. The capabilities for this type of water management already exist but it would be a radical departure from current policy and priorities. Construction on the floodplain has been encouraged by maintaining artificially low water releases during normal high water periods. Floodplain zoning laws and the use of easements would be required.

Controlled flooding could help maintain side channels and backwaters and redistribute organic matter stored in the sediments and in terrestrial environments so that more energy would flow through the food webs. Controlled flooding would also positively influence degradation and aggradation processes within the free-flowing reaches.

6) Structural modifications can be used as a management strategem to increase habitat diversity, secondary production, etc. Completed projects such as notched, rootless, and low elevation dikes and revetments in the channelized reach, have produced encouraging results. The backwater areas and chutes created by these structural modifications are also important rearing areas for some immature fish.

Even in the unchannelized river reaches in-channel structures may be helpful in creating habitats that have been lost by degradation of the channel bed. Backwater areas and subsidiary channels can be created by constructing sand-fill revetments which project into the river. These techniques have not been attempted on a large scale but have potential for maintaining and even increasing habitat diversity.

7) Introductions of nonindigenous fishes and crustaceans have occurred numerous times in the drainage basin. Generally these introductions were intended to fill new niches and habitats created in impoundments. *Osmerus mordax* were introduced into Sakakawea as forage for other introduced, cold water species of salmonids. *Osmerus mordax* quickly spread thoughout the middle Missouri River and currently occurs in all reservoirs except Fort Peck, but is abundant only in Sakakawea and Oahe which thermally stratify. They cannot survive the warmer summer temperatures in most river reaches but are temporally distributed thoughout the middle and lower Missouri River. These are only examples, many nonindigenous introductions have been made and few were made with careful analysis of the consequences to the native ichthyofauna. Future stockings should be carefully assessed by all basin states.

8) Many of the previous suggestions for maintaining and improving habitat diversity and managing the Missouri River fisheries involve a considerable expenditure of funds. Theoretically, mitigation plans for wildlife and fisheries could provide funds to accomplish some projects. However, none of the mitigation plans have been implemented on the Missouri River. Moreover, these plans have usually called for substituting upland terrestrial and lentic habitats for lost riparian floodplain and lotic habitats. A new funding approach is obviously needed but, in the interim, the diversion of monies from existing projects offers an immediate funding source for new projects. Among the prime candidates for funding donorships are those designed to maintain a navigable channel from the river's mouth to Sioux City, Iowa. The total estimated construction costs, attributed to bank stabilization and navigation structures was 427 million dollars and annual operating costs average 11.4 million dollars. Total commercial tonnage on the Missouri River currently averages 2.9 million t with only about 0.5 million t being transported over the 193 km reach between Sioux City and Omaha. Elimination of maintenance of this portion of the channelized river and the 35 km reach of river with stabilized banks upstream of Sioux City (Kensler's Bend Project) could free an estimated 2 million dollars annually for use in other projects. Realistically the entire Navigation–Bank Stabilization project of the P–S MBP has a 0.77 projected benefit-cost ratio when computed at a 7 3/8% interest rate. It would be fiscally prudent to terminate the entire project and use the savings in operating costs to fund other projects. This decision would be vigorously opposed but would not necessarily preclude navigation, at least in the lower reaches.

The future problems facing fishery managers are formidable and the solutions more political than operational. We cannot realistically return to a completely natural lotic ecosystem. We can, however, manage free-flowing river reaches so as to maintain existing habitat diversity and ameliorate deleterious effects upon aquatic communities. We can recover some of the elements of a natural hydrologic cycle. We can reestablish habitat types in unchannelized and channelized river reaches below the last mainstem dam. We can study and learn how each reach of the river integrates with the next. We can change the rates and perhaps the amounts of energy which flow between trophic levels. The opportunities and challenges of the future are seemingly endless. We can meet these challenges successfully only if our knowledge and preparation are adequate to influence major policy changes in water management.

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References

AMERICAN FISHERIES SOCIETY. 1982. Monetary values of freshwater fish and fish-kill counting guide. Special Publication No. 13. Bethesda, MD. 40 p.

ANON. 1983a. Catch and value of commercial fish. Mimeograph report, Iowa Conservatoin Commission, Des Moines, IA. 2 p.

1983b. South Dakota commercial fish catch for 1983. Mimeograph report, South Dakota Department of Game, Fish and Parks. Pierre, SD. 2 p.

BENSON, N.G. 1968. Review of fishery studies on Missouri River mainstem reservoirs. U.S. Dep. Interior, Bureau Sport Fish. Wildl. Res. Rep. No. 71: 61 p.

1980. Effects of post-impoundment shore modification on fish populations in Missouri River reservoirs. U.S. Fish Wildl. Res. Rep. N. 80. 32 p.

BENSON, N.G., AND B.C. COWELL. 1968. The environment and plankton density in Missouri River reservoirs, p. 358–373. *In* Reservoir Fishery Resources Symposium, Reservoir Committee, Southern Division, American Fisheries Society.

BERARD, E. 1985. Ecological investigations of the Missouri mainstem reservoirs in North Dakota. North Dakota Game and Fish Department, D-J report, Project F-2-R-31, Bismarck, ND. 97 p.

BERG, R.K. 1981. Fish populations of the Wild and Scenic Missouri River, Montana. Montana Department of Fish, Wildlife and Parks. Federal Aid to Fish and Wildlife Restoration Project. FW-3-R, Job 1a. Mimeo Report, Great falls, MT. 242 p.

BERNER, L.M. 1951. Limnology of the lower Missouri River. Ecology 32: 1–12.

BRAGG, T.B., AND A.K. TATSCHL. 1977. Changes in flood-plain vegetation and land use along the Missouri River from 1826 to 1972. Environ. Manage. 1(4): 343–348.

BROWN, C.J.D. 1971. Fishes of Montana. Big Sky Books, Montana State University, Bozeman, MT. 207 p.

BURCZYNSKI, J.G. MARRONE, AND P. MICHALETZ. 1985. Echo Surveys on Lake Oahe for rainbow smelt abundance estimation, July 1983 and July/August 1984. Biosonics, Inc., Seattle, WA. 89 P. + Append.

BURKE, T.D., AND J.W. ROBINSON. 1979. River structure modifications to provide habitat diversity. Presentation for the Mitigation Symposium, Colorado State University, Fort Collins, CO. July 16–20, 1979.

COWELL, B.C. 1970. The influence of plankton discharge from an upstream reservoir on standing crops in a Missouri River reservoir. Limnol. Oceanogr. 15: 427–441.

COWELL, B.C., AND P.L. HUDSON. 1967. Some environemental factors influencing benthic invertebrates in two Missouri River reservoirs, p. 541–555. *In* Reservoir Fishery

Resources Symposium. Reservoir Committee, Southern Division, American Fisheries Society.

Cross, F.B. 1967. Handbook of Fishes of Kansa. University of Kansas, Museum of Natural History, Miscellaneous Publication 45: 1–357.

Damann, K.E. 1951. Missouri River basin plankton study. Federal Security Agency, Public Health Service, Environmental Health Center, Cincinnati, OH. 100 p.

Farell, J.R. and M.A. Tesar. 1982. Periphytic algae in the channelized Missouri River with special emphasis on apparent optimal temperatures, p. 85–123. *In* L.W. Hesse et al. [ed.] The Middle Missouri River. The Missouri River Study Group, Norfolk, Nebraska.

Fisher, H.J. 1962. Some fishes of the lower Missouri River. Am. Midl. Nat. 68(2): 424–429.

Friberg, D.V. 1974. Investigation of paddlefish populations in South Dakota and development of management plans, 1972. South Dakota Department of Game, Fish and Parks, Project F-15-R-8, Report 74-21. Pierre. SD. 33 p.

Funk, J.L., and J.W. Robinson. 1974. Changes in the channel of the lower Missouri River and effects on fish and wildlife. Missouri Department of Conservation Aquatic Series No. 11. Jefferson City, MO. 52 p.

Gardner, W., and R.K. Berg. 1982. An analysis of the instream flow requirements for selected fishes in the wild and scenic portion of the Missouri River. Bureau of Land Management, Department of Interior, Lewistown, MT. 111 p.

Groen, C.L. and. J.C. Schmulbach. 1978. The sport fishery of the unchannelized and channelized middle Missouri River. Trans. Am. Fish. Soc. 107(3): 412–418.

Hanten, R.L. and A. Talsma. 1984. Fish stocking summary for Missouri River reservoirs. South Dakota Department of Game, Fish and Parks, Report Number 84-1. Pierre, SD. 15 p.

Harlan, J.R., and E.B. Speaker. 1956. Iowa fish and fishing (3rd ed.) Iowa Conservation Commission, Des Moines, IA. 324 p.

Hesse, L.W. 1979. Creel survey-Missouri River sport and commercial fishermen. Final report D J Project F-15-R Study II. Nebraska Game and Parks Commission, Norfolk, NE. 18 p.

1982. Missouri River fisheries management plan. Final Report D J Project No. F-15-R, Study IV. Nebraska Game and Parks Commission, Norfolk, NE. 7 p.

1983. Population estimates of channelized Missouri River fishes. Final report, National Marine Fisheries Service Project 2-359-R. Nebraska Game and Parks Commission, Lincoln, NE. 8 p.

1987. Taming the wild Missouri River: What has it cost? Fisheries 12(2): 2–9.

Hesse, L.W., G.L. Hergenrader, H.S. Levis, S.D. Reetz, and A.B. Schlesinger [ed.]. 1982a. The Middle Missouri River. A collection of papers on the biology with special reference to power station effects. The Missouri River Study Group, Norfolk, NE. 301 p.

Hesse, L.W., and J. Klammer. 1984. Ecology of unchannelized reaches of the Missouri River. D J Project Number F-75-R, Progress Report. Nebraska Game and Parks Commission, Norfolk, NE. 90 p.

Hesse, L.W. and G. Mestl. 1985. Ecology of unchannelized reaches of the Missouri River. D J Project Number F-75-R, Progress Report. Nebraska Game and Parks Commission, Norfolk, NE. 70 p.

Hesse, L.W., and B. Newcomb. 1982. On estimating the abundance of fish in the upper channelized Missouri River. N.A. J. Fish. Mange. 2: 80–83.

Hesse, L.W., B. Newcomb, and Schainost. 1982b. Movement, population estimation, CPE, mortality and harvest of Missouri River and tributary channel catfish. *In* L.W. Hesse [ed.]. The Missouri River channel catfish. Nebraska Technical Series No. 11. Norfolk, NE. 33–39.

Hesse, L.W., C.W. Wolfe, and N.K. Cole. 1986. Biological aspects of the unchannelized Missouri River and its habitats. 48th Midwest Fish and Wildlife Conference, Omaha, NE. 47 p.

Hoffman, G.R. 1978. Shore vegetation of Lakes Oahe and Sakakawea, mainstem Missouri River reservoirs. Project report. University of South Dakota, Vermillion, SD. 20 p.

Houtcooper, W.C., D.J. Ode, J.A. Peason, and G.M. Vandell III. 1985. Rare animals and plants of South Dakota. Prairie Nat. 17(3): 143–165.

Johnson, D.H. 1963. The food habits of the goldeye of the Missouri River and Lewis and Clark Reservoir South Dakota. M.S. thesis, University of South Dakota. Vermillion, SD. 36 p.

Johnson, W.C., R.L. Burgess, and W.R. Keammerer. 1976. Forest overstroy vegetation and environment on the Missouri River floodplain in North Dakota. Ecol. Monogr. 46: 59–84.

JONES, W.E., AND J.H. SELGEBY. 1974. Invertebrate macrobenthos of Lake Oahe, 1968–69. Technical Paper Number 73. U.S. Fish and Wildlife Service, Department of the Interior., 11 p.

Jones, D.J. 1963. The distribution of Nebraska fishes. Nebraska Game, Forestation, and Parks Commission. Lincoln, NE. 75 p.

Jordan, D.S. and S.E. Meek. 1885. List of fishes collected in Iowa and Missouri in August, 1884, with description of three new species. Proc. U.S. Nat. Mus. 8(1): 1–16.

Kallemeyn, L.W., and J.F. Novotny. 1977. Fish and fish food organisms in various habitats of the Missouri River in South Dakota, Nebraska, and Iowa. North Central Reservoir Investigations. Yankton, SD. FWS/OBS - 77/25, 100 p.

Lock, R.A. 1977. Nebraska's endangered and threatened wildlife. Nebraska Game and Parks Commission, Wildlife Report, Lincoln, NE. 35 p.

Lord, W.B., S.K. Tubbesing, and C. Althen. 1975. Fish and wildlife implication of upper Missouri Basin water allocation. Monograph Number 22, Program on Technology, Environment, and Man. Institute of Behavioral Science. University of Colorado, Boulder, CO. 114 p.

Martin, D.B., and J.F. Novotny, 1975. Nutrient limitation of summer phytoplankton growth in two Missouri River reservoirs. Ecology 56: 199–205.

1977. Zooplankton standing crops in the discharge of Lake Francis Case, 1966–72. Am. Midl. Nat. 98(2): 296–307.

Martin, D.B., J.F. Novotny, and G.K. O'Bryan. 1980. Limnology of four Missouri River Reservoirs Part I: physiochemistry and phytoplankton production. Proc. SD Acad. Sci. 59: 91–114.

McComish, T.S. 1967. Food habits of bigmouth and smallmouth buffalo in Lewis and Clark Lake of the Missouri River. Trans. Am. Fish. Soc. 96: 70–74.

McKenna, M.G., and R.W. Seabloom. 1979. Endangered, threatened and peripheral wildlife of North Dakota. Institution for Ecological Studies, Reserach Report 28, University of North Dakota, Grand Forks, ND. 62 p.

Michaletz, P.H., D.G. Unkenholz, and C.C. Stone. 1987. Prey size selectivity and food partitioning among zooplanktivorous age-0 fishes in Lake Francis Case, South Dakota. Am. Midl. Nat. 117(1): 126–138.

Miller, L.M. 1984. Angler harvest survey of Lake Francis Case, South Dakota. M.S. thesis, South Dakota State University, Brookings, SD. 66 p.

Miller, G.L., and W.R. Nelson. 1974. Goldeye in Lake Oahe: abundance, age, growth, maturity, food, and the fishery, 1963-69. U.S. Fish Wildl. Serv. Tech. Pap. 79.

Missouri Department of Conservation. 1984. Checklist of rare and endangered species of Missouri. Missouri Department of Conservation. Natural History Section. Jefferson City, MO. 16 p.

Missouri River Basin Commission. 1980. Plan of study, Missouri River basin hydrology study. Omaha, NE. 91 p.

1977. The Missouri River basin water resources plan. Omaha, NE. 206 p.

Modde, T.C., and J.C. Schmulbach. 1973. Seasonal changes in the drift and benthic macroinvertebrates in the unchannelized Missouri River in South Dakota. Proc. Acad. Sci. 52: 118–126.

Morris, L. 1966. Flathead catfish investigations in the Missouri River. Nebraska Game and Parks Commission, DJ Project F-4-R-11, Job 23, Lincoln, NE. 51–54.

Morris, L.A., R.N. Langemeier, T.R. Russell, and A. Witt, Jr. 1968. Effects of mainstem impoundments and channelization upon the Missouri River, Nebraska. Trans. Am. Fish. 97(4): 380–388.

Morris, J., L. Morris, and L. Witt. 1974. The fishes of Nebraska. Nebraska Game Parks Commission, Lincoln, NE. 100 p.

Nelson, W.R. 1961. Report of fisheries investigations during the eighth year of impoundment of Ft. Randall Reservoir, South Dakota, 1960. South Dakota Department of Game, Fish and Parks, DJ Project F-1-R 10, Report 61-2, Pierre, SD. 61 p.

Nelson, W.R., R.E. Siefert, and D.V. Swedberg. 1968. Studies on the early life histories of resevoir fishes, p. 374-385. *In* Reservoir Fishery Resources Symposium. Reservoir Committee, Southern Division, American Fisheries Society.

Newcomb, B.A. 1985. Population estimates of lower channelized Missouri river commercial fish. Nebraska Game and Parks Commission, Progress Report, National Marine Fisheries Service Project 2-402-R, Lincoln, NE. 13 p.

Nord, A. E., and J. C. Schmulbach. 1973. A comparison of macroinvertebrate aufwuchs in the unstabilized and stabilized Missouri River. Proc. SD Acad. Sci. 52: 127–139.

Personius, R.G. and S. Eddy. 1955. Fishes of the Little Missouri River. Copeia (1): 41–43.

Pflieger, W.L. 1971. A distributional study of Missouri fishes. Musuem of Natural History, University of Kansas, Publication 20(3): 225–570, Lawrence, KS.

1975. The fishes of Missouri. Missouri Department of Conservation, Columbia, MO. 343 p.

Reetz, S.D. 1982. Phytoplankton studies in the Missouri River at Fort Calhoun Station and Cooper Nuclear Station, p. 71–83. *In* L.W. Hesse et al. [ed.]. The Middle Missouri River. The Missouri River Study Group, Norfolk, NE.

Repsys, A.J., and G.D. Rogers. 1982. Zooplankton studies in the channelized Missouri River, p. 125–145. *In* L.W. Hesse et al. [ed.] The Middle Missouri River. The Missouri River Study Group, Norfolk, NE.

Riis, J. C. 1983. Walleye movement and angler use on Lake Oahe, South Dakota, 1982. South Dakota Department of Game, Fish and Parks, Progress Report 83-11, Pierre, SD. 8 p.

1985. Walleye movement, harvest, and angler use on Lake Oahe, 1981–1984. South Dakota Department of Game, Fish and Parks, Completion Report 84-4, Pierre, SD. 8 p.

1986. Angler harvest survey on Lake Sharpe, South Dakota 1984–1985. South Dakota Department of Game, Fish and Parks. Pierre, SD.

Risotto, S.P. and R.E. Turner. 1985. Annual fluctuation in abundance of the commercial fisheries of the Mississippi River and tributaries. Fish. Manage. 5: 557–574.

Robins, C.R., R.M. Bailey, C.E. Bond, J.R. Brooker, E.A. Lachner, R.N. Lea, and W.B. Scott. 1980 A list of common and scientific names of fishes from the United States and Canada, 4th ed. Am. Fish. Soc. Spec. Publ. No. 12. Bethesda, MD. 174 p.

Robinson, J.W. 1985. Missouri's commercial fishery harvest; 1979, 1980, 1981, 1982, and 1983. Final Report, National Marine Fisheries Service Project 2-363-R. Missouri Department of Conservation. Columbia, MO. 26 p.

Roosa, D.M. 1977. Endangered and threatened fish of Iowa. Special report No. 1, Preserves Board of Iowa, Des Moines, IA. 25 p.

Rosen, R.A. 1976. Distribution, age and growth, and feeding ecology of paddlefish in unaltered Missouri River, South Dakota. M.S. thesis, State University, Brookings, SD. 95 p.

Ruelle, R. 1971. Factors influencing growth of white bass in Lewis and Clark Lake, p. 411–423 *In* G.E. Hall [ed.] Reservoir fisheries and limnology. American Fisheries Society, Bethesda, MD.

Sayre, W.W., and J.F. Kennedy. 1978. Degradation and aggradation of the Missouri River. Iowa Institute of Hydraulic Research, University of Iowa, Iowa City, IA. 67 p.

Schainost, S. 1981. Population dynamics of the commercial fishery resource of the unchannelized and stabilized Missouri River. Final Report, National Marine Fisheries Service Project 2-275-R. Nebraska Game and Parks, Lincoln, NE. 100 p.

Schmidt, B.R. 1975. Results and evaluation of an aerial creel survey technique on Lake Sharpe, South Dakota. M.S. thesis, South Dakota State University, Brookings, SD.

Schmulbach, J.C., G. Gould, and C.L. Groen. 1975. Relative abundance and distribution of fishes in the Missouri River, Gavins Point Dam to Rulo, Nebraska. Proc. SD Acad. Sci. 54: 194–222.

Schmulbach, J.C., and H.A. Sandholm 1962. Littoral bottom fauna of Lewis and Clark Reservoir. Proc. SD Acad. Sci. 41: 101–112.

Schuckman, J.J. 1982. Population estimates of shovelnose sturgeon *Scaphirhynchus platorynchus* in the unchannelized Missouri River. M.A. thesis, University of South Dakota, Vermillion, SD. 41 p.

Shields, J.T. 1955. Report of fisheries investigations during the second year of impoundment of Ft. Randall reservoir, South Dakota, 1954. South Dakota Game, Fish, and Parks, DJ Project F-1-R-4, Job 6, Pierre, SD. 100 p.

1956. Report of fishery investigations during the third year of impoundment of Ft. Randall reservoir, South Dakota, 1955. South Dakota Game Fish and Parks, DJ Project F-1-R-5, Job 2, Pierre, SD. 91 p.

Slizeski, J.J., J.L. Andersen, and W.G. Dorough. 1982. Hydrologic setting, system operation, present and future stresses, p. 15–37. *In* L.W. Hesse et al. [ed.]. The Middle Missouri River. The Missouri River Study Group, Norfolk, NE. 301 p.

Starostka, V.J., and W.R. Nelson. 1974. Age, growth, sexual maturity, and food of channel catfish in central Lake Oahe, 1968–1969. U.S. Fish Wildl. Serv. Tech. Pap. 81: 15 p.

Stephen, J. 1984. Kansas marketable fisheries investigations. National Marine Fisheries Service Project 2-401-R, annual progress report, Pratt, KS. 16 p.

Stewart, P. A. 1983. Lower Missouri River Basin fishery investigations. D J Project FW-2-R-12 Progress Report, Montana Department of Fish, Wildlife and Parks, Fort Peck, MT. 44 p.

Stone, C.C. 1985a. Angler use and sport fishing harvest survey on Lake Francis Case, South Dakota 19834. South Dakota Department of Game, Fish and Parks. Report 85-1. Pierre, SD. 26 p.

1985b. Lewis and Clark Lake fishing and hunting use survey, 1984. South Dakota Department of Game, Fish and Parks, Report 85-2, Pierre, SD. 44 p.

Swanson, G.A. 1967. Factors influencing the distribution and abundance of *Hexagenia* nymphs (Ephemeroptera) in a Missouri River reservoir. Ecology 48(2): 216–225.

TODD, R.D., AND J.F. BENDER. 1982. Water quality characteristics of the Missouri River near Fort Calhoun and Cooper Nuclear Stations, p. 39–68. *In* L.W. Hesse, et al. [ed.]. The Middle Missouri River. The Missouri River Study Group, Norfolk, NE.

TONDREAU, R. 1982. Results of flathead catfish population study, 1982. Aquatic Studies Report. Morningside College, Sioux City, IA. 16 p.

TONDREAU, R.L., J. HEY, AND E. SHANE. 1983. Missouri River aquatic ecology studies ten year summary (1972–1982). Morningside College, Sioux City, IA. 71 p.

TROELSTRUP, N.H., JR. 1985. Macroinvertebrate colonization and consumer food habits in the Missouri River of northeastern Nebraska. M.S. thesis, University of Nebraska, Lincoln, NE. 180 p.

UNKENHOLZ, D.G., P.H. MICHALETZ, AND C.C. STONE. 1981. Fisheries studies related to the Gregory county pumped storage project. Progress Report 81-8. South Dakota Department of Game, Fish and Parks, Pierre, SD. 80 p.

1983. Fisheries studies related to the Gregory county pumped storage project. Progress Report 82-8. South Dakota Department of Game, Fish and Parks, Pierre, SD. 80 p.

1984. Fisheries studies related to the Gregory county pumped storage project. Progress Report 84-5. Department of Game, Fish and Parks, Pierre, SD. 80 p.

U.S. ARMY CORPS OF ENGINEERS. 1979. Master Manual: Missouri River mainstem reservoir system reservoir regulation manual. U.S. Army Engineering Division, Omaha, NE. 200 p.

1980. Investigation of channel degradation. Missouri River Gavins Point Dam to Platte River Confluence. Engineering Division, Omaha District, Omaha, NE. 92 p. and Appendices A thru D.

1985. Missouri River mainstem reservoirs. Summary of actual 1984–85 operations and operating plan for 1985–86. Omaha, NE. 100 p.

U.S. DEPARTMENT OF INTERIOR. 1979. Missouri national recreational river management plan. Heritage Conservation and Recreation Service. Washington, DC. 77 p.

U.S. FISH AND WILDLIFE SERVICE. 1980. Missouri River stabilization and navigation project Sioux City, Iowa to mouth. Coordination Act Report U.S. Fish and Wildlife Service, Kansas City, MO. 85 p.

1985. Missouri River bibliography. Ecological Services, Pierre, South Dakota. 60 p.

1986. Endangered and threatened wildlife and plants, Title 50 CFR 17.11 and 17.12, Washington, D.C. 30 p.

U.S. HOUSE DOCUMENT NO. 475. 1944. U.S. House of Representatives, U.S. Government Printing Office, Washington, D.C. 32 p.

WALBURG, C. H. 1976. Changes in the fish population of Lewis and Clark Lake, 1956–74, and their relation to water management and the environment. U.S. Fish and Wildlife Research Report 79: 34 p.

1977. Lake Francis Case, a Missouri River reservoir: Changes in the fish population in 1954–75 and suggestions of management. U.S. Fish and Wildlife Technical Paper No. 95: 32 p.

WALBURG, C.H., AND W.R. NELSON. 1966. Carp, river carpsucker, smallmouth buffalo and bigmouth buffalo in Lewis and Clark Lake, Missouri River. Bureau of Sport Fisheries and Wildlife Research Report 69: 30 p.

WARD, J. V. 1976. Effects of flow patterns below large dams on stream benthos: a review, p. 235–253. *In* J. F. Orsborn and C. H. Allman [ed.] Instream flow needs. Vol. II. Western Division, American Fisheries Society, Bethesda, MD.

WARNICK, D. C. 1977. Commercial fishing or rough fish control in South Dakota, some views and apparent values. Bulletin Number 7. South Dakota Department of Game, Fish and parks, Pierre, SD. 23 p.

WIEDENHEFT, W. D. 1984. Establishment of aquatic baselines in large inland impoundments. Interim Report National Marine Fisheries Service Project 1-123-R. Montana Department of Fish, Wildlife and Parks, Great Falls, MT. 41 p.

WILLOCK, T. A. 1969. Distributional list of fishes in the Missouri drainage of Canada. J. Fish. Res. Board Can. 26: 1439–1449.

WRIGHT, K. J. 1970, The 1967–68 Sport fishery of the upper Mississippi River. Upper Mississippi River Conservation Committee, LaCrosse, WI. 116 p.

ZUERLEIN, G. 1985. Nebraska commercial fishery statistics, the Missouri River. Interim Report National Marine Fisheries Service Project 2-402-R. Nebraska Game and Parks Commission, Lincoln, NE. 56 p.

The Tennessee River

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Abstract

VOIGTLANDER, C.W., AND W.L. POPPE. 1989. The Tennessee River, p. 372-384. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The Tennessee River flows for 1 045 km through a drainage basin of 106 000 km^2. Today, the Tennessee River system, consisting of the mainstream Tennessee and its major tributaries, is fully controlled by a series of 40 dams, creating 264 000 ha of impounded surface water and a total impounded volume of $29.8 \times 10^9 m^3$. Tributary reservoirs differ significantly from mainstream reservoirs in morphometry and hydraulics; moreover, anthropogenic effects are substantially different in character and magnitude between the two sets of reservoirs. The system, which is managed principally for hydroelectric power, flood control and commercial navigation, supports a temperate, warmwater fish fauna dominated by clupeids, centrarchids, catostomids, and ictalurids. Mean total standing stock biomass ranges from 85 to 915 kg•ha^{-1}, of which from 30 to 70% is clupeid biomass. The aquatic system, including fisheries resources, is subject to four major stresses: low dissolved oxygen in hydrogeneration releases, point source pollution, non-point source pollution, and cultural eutrophication.

Résumé

VOIGTLANDER, C.W., AND W.L. POPPE. 1989. The Tennessee River, p. 372-384. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Le Tennessee s'écoule sur 1 045 km dans un bassin hydrographique de 106 000 km^2. Le réseau hydrographique du Tennesse, constitué du fleuve lui-même et de ses tributaires importants, est maintenant complètement endigué après la construction de 40 barrages qui ont créé des plans d'eau de 264 000 ha pour un volume total de $29{,}8 \times 10^9 m^3$. Les réservoirs des tributaires diffèrent beaucoup des réservoirs du cours principal, tant par la morphométrie que par l'hydraulique; de plus, les effets anthropiques diffèrent nettement en caractère comme en importance entre ces deux types de réservoirs. Ce réseau, aménagé principalement pour la production d'hydro-électricité, le contrôle des crues et la navigation commerciale, abrite des populations de poissons de climats tempérés qui vivent dans les eaux tièdes et qui sont dominés par les clupéidés, les centrarchidés, les catostomidés et les ictaluridés. La biomasse totale moyenne du stock actuel varie entre 85 et 915 kg• ha^{-1}; 30 à 70% de ce total est constitué de la biomasse des clupéidés. Le réseau, y compris les pêcheries, est exposé à quatre grands stress: une faible teneur en oxygène dissous à proximité des sources hydro-électriques, la pollution ponctuelle, la pollution non ponctuelle et l'eutrophisation d'origine agricole.

Characteristics of the System

The Tennessee River, formed by the confluence of the Holston and French Broad Rivers, has its origin in the western Appalachian mountains of Virginia and North Carolina and flows for 1 045 km to the mouth, joining the Ohio River in western Kentucky (Fig. 1). The drainage basin, comprising 106 000 km^2, is formed by a complex of physiographic provinces or regions ranging from the Ridge-and-Valley province in the northeast to the Highland Rim and Interior Coastal Plain in the west. Average annual precipitation is 132 cm; historic extremes (1890 through 1980) range from 96 to 165 cm. Of the total precipitation, approximately 51 cm (39%) occurs in winter months (December through March), when vegetative cover is least; overall, 55 cm (42%) is contributed to surface waters as runoff.

Prior to the creation of the Tennessee Valley Authority (TVA) in 1933, the Tennessee River and its major tributaries were uncontrolled. Average historic flow at the mouth of the Tennessee was 1 811 m^3•s^{-1}; extremes ranged from 127 m^3•s^{-1} to 13 000 m^3•s^{-1}, with flows directly proportional to seasonal runoff. The river, the fifth largest in the United States with regard to discharge, was not commercially navigable. Limiting depths for navigation were 0.5 m from Knoxville, Tennessee to Muscle Shoals, Alabama, and 1.3 m from Muscle Shoals to the river mouth at Paducah, Kentucky (Lesesne 1974); early attempts in the 1800's to improve navigation were unsuccessful (TVA 1936).

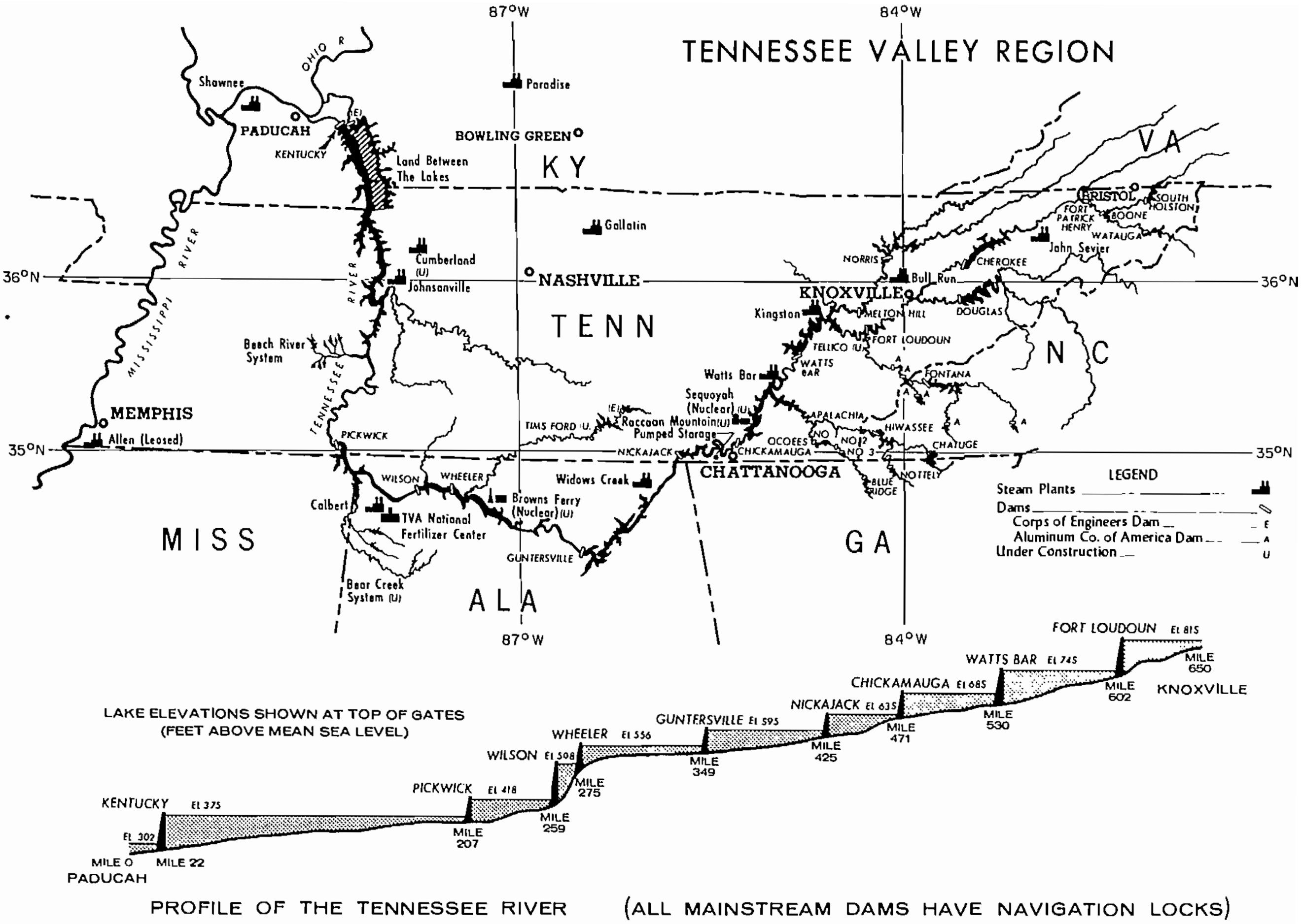

FIG. 1. The Tennessee River. Mainstream reservoirs are shown in profile. The Tennessee and Cumberland Rivers are connected by a canal located approximately 4.8 km upstream from Kentucky Dam.

Development of the Reservoir System

Upon its formation, TVA had three major priorities: flood control, providing a navigation channel, and production of hydroelectric power. These, together with programs for fertilizer research and development, erosion control, and reforestation were aimed at the general objective of improving the economically depressed region through agricultural and industrial development (McCarthy and Voigtlander 1983).

Between 1933 and 1944, TVA constructed 16 dams; this effort, when combined with two existing mainstream dams, essentially impounded the Tennessee and the majority of its major tributaries, thus providing the basic framework for the flood control system and a navigation channel of minimum 3.4 m depth from the Ohio River to Knoxville. In 1933, estimated surface water area in the Tennessee River System was 46 900 ha; all but a small portion of this was provided by the Tennessee River proper and its tributary streams. The construction of the system, which now totals 40 dams (36 TVA dams, 4 Aluminum Company of America (ALCOA) dams), has impounded approximately 264 000 ha. The total volume of water impounded at full pool is approximately 29.8 × 10^9m^3, which includes some 16.9 × 10^9m^3 of useful flood-control storage. Of the TVA dams, nine are mainstream dams (Fig. 1) which include navigation locks; two tributary reservoirs (Melton Hill — lock; Tellico — bypass canal) also provide for navigation, while the remainder are managed principally for flood control and hydrogeneration.

Operation of the System

Beyond the use and control of the system for flood control and maintenance of navigational depths, TVA operates an electrical generating system consisting of 29 hydroelectric dams (providing 3 300 megawatts), 12 coal-fired steam-electric plants (17 600 mw), 2 nuclear-powered steam-electric plants (5 900 mw) and 1 pumped-storage hydroeletric plant (1 500 mw). The four Alcoa dams in the TVA system provide another 300 mw. The 14 steam-electric plants provide base-load electrical power; these in sum require 67 × 10^6 m^3• d^{-1} of water (about 0.2% of reservoir system volume) to meet condenser cooling requirements at maximum capacity. Additional flows are occasionally necessary to maintain compliance with environmental or safety requirements during climatic extremes, e.g., heat waves or drought. Hydroelectric facilities supplement base-load generation when necessary and otherwise are operated to meet peak-load demands. Peak-load demands occur twice daily (early morning and late

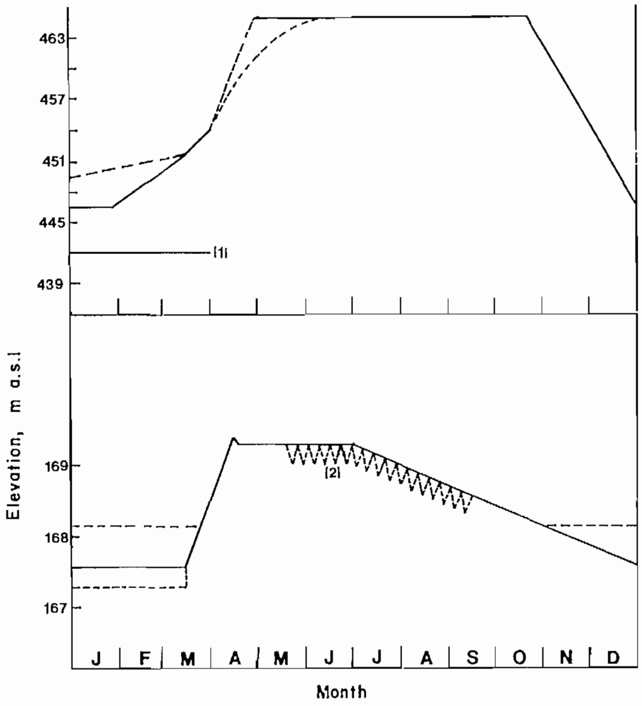

FIG. 2. Annual cycles of reservoir water-level control for a tributary storage reservoir (top) and a mainstream reservoir (bottom). Elevation is meters above mean sea level. Solid lines are the normal pattern; dashed lines identify optional levels that may be used during flood control operations. (1)=normal minimum pool; (2)=fluctuations employed for mosquito control.

afternoon). Seasonal peak loads occur in midwinter (heating) and midsummer (air conditioning). Water needs for electrical generation are integrated with the annual cycle of flood-control reservoir manipulation. This flood control cycle generally involves the gradual reduction of reservoir volumes during early autumn to achieve early-winter minimum pool levels and hence, maximum storage capacity (Fig. 2). Following the season of high flood probability (mid-December through mid-April) reservoirs are allowed to stabilize at normal full summer pools.

Because of their morphometry (Table 1) and the necessity of maintaining adequate depth for commercial navigation, mainstream reservoirs experience less dramatic water-level fluctuations (typically from 0.6 to 2.3 m) than do tributary or storage reservoirs (5 to 18 m).

Major Stresses

Major stresses on the Tennessee River aquatic system are: (1) low dissolved oxygen in reservoir releases, (2) point source pollution, (3) non-point source pollution and (4) eutrophication. Table 2 summarizes the Tennessee River reservoirs affected.

Low dissolved oxygen (DO) — A 1978 analysis by TVA concluded that releases from 18 dams contained DO concentrations significantly lower than State criteria, resulting in approximately 480 km of river being adversely affected. A recent analysis by the State of Tennessee (TDHE 1986) shows that releases from 10 TVA dams failed to the meet the State DO standard (5 mg • L^{-1}) and that 5 of these released water containing less than 1 mg • L^{-1}.

Point source pollution — At least five TVA reservoirs in Tennessee have been found to contain traces of toxic chemicals. Mercury contamination continues to exist in several areas as the result of historic releases, and in spite of clean-up efforts. PCB contamination has been documented for Fort Loudoun and Wilson Resevoirs; current investigations may document similar contamination in others. Nickajack Reservoir is contaminated by toxic organic chemicals, some apparently emanating from hazardous waste dumpsites.

TABLE 1. Morphometric Characteristics, TVA Reservoirs.

Reservoir	Outflow rate, $m^3 \cdot s^{-1}$	Volume, 10^6 m^3	Area, 10^6 m^2	Maximum depth, m	Mean depth, m	Length, km	Residence time, days
			Mainstream				
Kentucky	2403	2900	648.7	32.5	4.5	298	14.0
Pickwick	1970	1050	174.4	23.4	6.0	84	6.2
Wilson	1871	777	62.7	29.5	12.4	32	4.8
Wheeler	1741	1202	271.5	19.3	4.4	113	8.0
Guntersville	1427	1105	274.8	17.6	4.0	122	9.0
Nickajack	1203	288	42.0	17.7	6.9	74	2.8
Chickamauga	1154	614	143.3	24.2	4.3	95	6.2
Watts Bar	975	1081	159.4	22.5	6.8	116	12.8
Fort Loudoun	470	399	59.1	26.1	6.8	77	9.8
			Tributary				
Chatuge	16.5	227	28.5	33.0	8.0	19	159
Cherokee	158.6	1084	122.6	38.8	8.8	77	79
Douglas	230.9	848	123.0	28.9	6.9	75	43
Fontana	133.4	1183	43.1	123.3	27.4	50	103
Hiwassee	71.6	344	24.6	65.4	14.0	39	56
Norris	145.5	1715	138.4	54.2	12.4	54	136
South Holston	35.1	609	30.7	67.8	19.8	36	201
Tims Ford	33.5	592	42.9	41.9	13.8	55	205
Watauga	25.7	558	26.0	76.0	21.5	26	251

TABLE 2. Tennessee River system reservoirs having identified water quality problems. For low dissolved oxygen, 1 = releases less than 1 mg• L^{-1}; 2 = releases less than 5 mg• L^{-1}; 3 = Others not classified by TDHE (1986). See text for details.

	Low dissolved oxygen			Toxic organics and heavy metals	Non-point sources	Eutrophication	
	1	2	3			TDHE	TVA
				Mainstream			
Fort Loudoun		X		X		X	
Watts Bar		X				X	
Chickamauga				X			
Nickajack				X			
Guntersville							X
Wheeler			X	X			X
Wilson			X	X			
Pickwick			X	X			
Kentucky				X		X	
				Tributary			
Fort Patrick Henry		X				X	
South Holston	X						
Watauga		X					
Boone		X				X	
Cherokee	X			X		X	
Norris	X						
Nolichucky					X		
Douglas	X						X
Ocoee No. 1					X		
Ocoee No. 2					X		
Normandy							X
Tims Ford	X						
Upper Bear Creek					X		

Because the majority of toxic organic and heavy metal pollutants have not been subject to systematic surveys and analyses, the true extent of the problem is unknown.

Non-point source pollution — TVA has identified 12 reservoirs as having impaired uses (e.g., fishing, recreation, water supply), in which non-point source pollution is a major contributing factor. The sources of such pollution appear to be runoff from mined lands (coal, mica, and feldspar), nutrient loads in agricultural runoff, and, to a lesser extent, urban runoff.

Eutrophication — While reservoirs do not undergo precisely the same ageing process as natural lakes, and are not as sensitive to high nutrient levels, they can and do exhibit the classical symptoms of eutrophication. In the case of reservoirs in the Tennessee Valley, eutrophication can be considered as the summation response to the spectrum of point and non-point source nutrient input. Seven TVA reservoirs have been identified as being affected by cultural eutrophication; six TVA reservoirs in Tennessee have been characterized as eutrophic, based on chlorophyll *a* concentration. The trend of increasing cultural eutrophication is likely to continue, owing to the lack of environmental regulation regarding non-point source pollution and the resistance to implementing effective controls in the absence thereof.

Physical Management Practices

Water uses below Tennessee River and tributary river dams, are directly and significantly influenced by dam operation. Many river reaches below the dams only marginally support fisheries and other aquatic life, and may also lack the capability to sufficiently assimilate wastes. The primary concerns have been low dissolved oxygen (DO) concentrations, intermittent stream flows owing to sporadic discharges from dams, and occasionally high concentrations of iron, dissolved manganese and sulfide. These problems have been addressed aggressively in the past 5 years on the Tennessee River and its tributaries (Davis et al. 1983; Bohac et al. 1986).

Three separate, but interlocking approaches have been used. These are: (1) installation of hub baffles on Francis Wheel-type hydroturbines, (2) construction of gabion reregulation weirs, and (3) in-reservoir destratification and hypolimnetic aeration devices.

Although hub baffles have been used to provide significant increases in DO, they are not applicable to all Francis turbines. In cases where they were ineffective, physical and mathematical models have not proven satisfactory when applied to a prototype turbine. In cases where hub baffles could not be used, compressed air has been used to significantly increase DO concentrations in release waters. Unfortunately, compressed air injection is more expensive than hub baffle installation, but compares favorably with high-purity oxygen injection.

Instream flow improvements are currently being evaluated below Norris Dam on the Clinch River, one of the major tributaries to the Tennessee. Discharges from Norris Dam, while sufficiently cold to support a put-grow-and-take trout fishery (rainbow trout, *Oncorhynchus mykiss* and brown trout, *Salmo trutta*, are deficient in DO for several months each year. This combined with intermittent flow (1.4 m^3 • s^{-1} under conditions of hydrogeneration to 240 m^3 • s^{-1} under full, two-turbine generation) severely limits both benthic production and suitable trout habitat. A gabion structure weir constructed of galvanized steel baskets filled with 10–20 cm washed limestone rock was placed 3 km below Norris Dam to provide flow regulation. The structure is 1.5 m high, 6.4 m wide and 129 m long and contains 54, 30-cm steel pipes equipped with float valves which control disharge from the weir; the system was designed to provide continuous minimum flow at 5.7 cm • s^{-1}. Although the evaluation of the weir, especially in terms of positive impacts on the biological community, has not been concluded, the structure has met most design objectives and early results with respect to improvement of downstream DO concentrations and development of a more diverse and productive benthic community are promising.

In-reservoir hypolimnetic aeration and destratification devices are also currently being evaluated. Poppe (1984) evaluated full destratification and hypolimnetic aeration in full water column, open-ended enclosures with regard to their effectiveness in minimizing releases of nutrients and metals from the sediment and improving water-column DO conditions. Both full and partial mixing were successful in reducing the formation of dissolved iron and manganese. Dissolved inorganic nitrogen and DO concentrations became uniform throughout the fully mixed system with definite chemical stratification obvious in the hypolimnetic aeration system.

Subsequently, one hypolimnetic aeration device and one desratification device have been placed in two separate tributary reservoirs in order to determine whole water-body effects. Results of these investigations should be available in 1987.

Nutrient Inflows and Outflows

Nitrogen (N) and phosphorus (P) inflows and outflows, along with hydraulic discharge, were recorded weekly for the period 1958–77 for the 18 reservoirs described in Table 1. Throughout the years of intense eutrophication analyses, these data were examined continuously and serve as the baseline data for identifying water quality improvements or degradation in the Tennessee Valley. A portion of these data (1974 through 1976) appear in Table 3; a complete description of the data set appears in Higgins et al. (1980). Local inflows (Table 3) averaged 9.9 and 39.9 % of the total inflow for mainstream and triburary reservoirs, respectively. Concentrations of N and P for the local inflows were estimated from available tributary data within the watershed. The N and P contributions of large wastewater treatment plants which discharge directly to a reservoir were estimated from average effluent concentrations and flows.

Tributary reservoirs generally retain a greater portion of inflowing N and P than do mainstream reservoirs, as would be expected owing to greater water retention times. Negative N and P retention values were observed in several of the mainstream reservoirs and in one tributary reservoir. This may be due to flushing caused by higher than normal flows during the 1974–76 period (flows averaged from 15 to 32 % above the 1958–77 averages except for Tims Ford, which had flows slightly less than normal). It is also possible that the method used to calculate local N and P inflows underestimated the contribution of point and non-point sources along industrialized sections of the Tennessee River. Although non-point source nutrient contributions have recently become a concern in the Tennessee Valley

TABLE 3. Mean P and N inflows and outflows
Selected date 1974–76.

Reservoir	Phosphorus					Nitogen				
	Inflow mg• L^{-1}	Outflow mg• L^{-1}	Inflow load 10^3kg• d^{-1}	Outflow load 10^3kg• d^{-1}	Net load 10^3kg• d^{-1}	Inflow mg• L^{-1}	Outflow mg• L^{-1}	Inflow load 10^3kg• d^{-1}	Outflow load 10^3kg• d^{-1}	Net load 10^3kg• d^{-1}
Kentucky	0.074	0.075	15.03	15.65	−0.62	0.717	0.626	145.0	130.1	14.9
Pickwick	0.051	0.064	8.70	10.93	−2.23	0.709	0.731	120.3	124.4	−4.1
Wilson	0.056	0.052	8.99	8.36	0.63	0.685	0.713	110.7	115.2	−4.5
Wheeler	0.035	0.056	5.24	8.41	−3.17	0.618	0.674	92.9	101.3	−8.4
Guntersville	0.038	0.029	4.71	3.59	1.12	0.654	0.596	80.5	73.4	7.1
Nickajack	0.036	0.035	3.71	3.67	0.04	0.623	0.626	64.7	65.1	−0.4
Chickamauga	0.026	0.027	2.55	2.70	−0.15	0.575	0.595	57.2	59.3	−2.1
Watts Bar	0.040	0.027	3.34	2.25	1.09	0.739	0.610	62.0	51.3	10.7
Fort Loudoun	0.044	0.050	1.80	2.03	−0.23	1.033	0.880	41.9	35.7	6.2
Chatuge	0.021	0.016	0.030	0.023	0.007	0.360	0.268	0.5	0.4	0.1
Cherokee	0.155	0.033	2.068	0.450	1.618	1.424	1.050	19.0	14.4	4.6
Douglas	0.067	0.033	1.316	0.666	0.650	0.722	0.813	14.1	16.2	−2.1
Fontana	0.045	0.015	0.509	0.171	0.338	0.581	0.369	6.5	4.3	2.2
Hiwassee	0.021	0.017	0.127	0.105	0.022	0.343	0.292	2.1	1.8	0.3
Norris	0.038	0.014	0.446	0.177	0.269	0.944	0.590	11.2	7.4	3.8
South Holston	0.034	0.011	0.103	0.033	0.700	0.732	0.713	2.2	2.2	0.0
Tims Ford	0.024	0.022	0.067	0.065	0.002	0.721	0.576	2.0	1.7	0.3
Watauga	0.051	0.012	0.108	0.027	0.081	0.724	0.606	1.5	1.3	0.2

Loads were calculated quarterly from daily flow records and monthly P and N measurements. Mean concentrations were calculated by dividing total loads for the 1974–76 period by total flow volumes.

TABLE 4. Ecological characteristics of mainstream and tributary reservoirs of the Tennessee River system. Adapted from Placke (1983) and Barr (1978).

Mainstream	Tributary
Trophic potential	
Retention short (~10 d)	Long (~138 d)
Shallow (6.6 m)	Deep (18.1 m)
Stratification weak, inconsistent	Strong
High turbidity Secchi depth 1.2 m	Low, Secchi depth 2.5 m
Constant alkalinity (43 - 60 mg• L^{-1})	Variable (4.6 - 82.6 mg• L^{-1})
High unit P load, low P retention, high in-reservoir concentration (31 g• m^{-2}• yr^{-1}, -0.08, 0.01 - 0.02 mg• L^{-1})	Lower unit P load, higher retention, lower in-reservoir concentration (4 g• m^{-2}• yr^{-1}, 0.48, <0.01 mg• L^{-1})
Trophic response	
Chlorophyll production limited primarily by light and hydraulics	Production stongly correlated with P and N
Significant algae and macrophyte problems in some reservoirs	Largely free of macrophytes, owing to periodic drawdowns
Formerly diversified algal flora, but trending to cyanophyte dominance	Cyanophyte dominance in midsummer (one exception — Norris)
Fish community	
Number of species high (30 - 55 occurring in more thant 10% of samples)	Fewer species (<30)
High prey: predator biomass ratio (2.6 - 3.6)	Lower, more variable prey: predator biomass ratio (0.4 - 3.0)
Higher standing stock biomass; higher % clupeids, sciaenids, ictalurids, catostomids	Lower standing stock biomass; higher % *Micropterus*, *Pomoxis*, percids, cyprinids

Region, the great majority of N and P contribution to the system is a result of cultural eutrophication.

Biology of the System

Reservoirs in the Tennessee River system are categorized according to their principal function and location as either mainstream or tributary reservoirs. Although it is becoming apparent from several recent investigations that definite subsets exist within these two broad categories, some generalizations can be made regarding biological characteristics. Mainstream reservoirs are more riverine in morphometry and behave more like large rivers in terms of stratification and primary production (Table 4), whereas tributary reservoirs behave more like lakes.

Aquatic Macrophytes

Eurasian watermilfoil (*Myriophyllum spicatum*) presently infests over 5 500 ha at various densities in eight reservoirs, while spinyleaf naiad (*Najas minor*) occupies about 3 100 ha in six reservoirs. Mixtures of the two species infest an additional 730 ha. Together, these exotic species comprise about 95% of the total weed infestation. *Hydrilla*, which was discovered in Guntersville Reservoir in 1982, is spreading and is expected to become a major problem in the near future. Another localized problem is caused by native American pondweed (*Potamogeton nodosus*). It generally occupies areas where other species have been reduced by chemical treatment. Several other troublesome infestations occur, e.g., Southern naiad (*Najas guadalupensis*), coontail (*Ceratophyllum demersum*), Uruguayan waterprimrose (*Ludwigia uruguayensis*), Brazilian elodea (*Egeria densa*) and muskgrass (*Chara* sp.), but these are localized and involve only small areas.

An integrated approach (Burns et al. 1984) has been adopted to control the spread of aquatic plants and to complement the full range of Tennessee River water uses. Water-level manipulations supplemented by herbicide treatments are used to control excessive infestations and to deter the spread of *Hydrilla* and other noxious plants. Support studies (e.g., mechanical and biological control and alternative application techniques) are also conducted to determine efficacy, cost-effectiveness and environmental compatability.

Water level fluctuations have been an effective method for controlling some weed infestations, Winter drawdowns effectively "freeze out" plants, especially perennial species such as watermilfoil. Summer drawdowns have been designed to subject naiads within the drawdown zone to drying before peak seed production occurs. Results of this practice are currently being evaluated with respect to long-term effectiveness. Various other techniques are currently in use or are being evaluated; these include (1) plant competition, (2) use of alligatorweed flea beetles (*Agasicles* sp.) and alligatorweed thrips (*Amynothrips* sp.), (3) mechanical harvesting, (4) screen barriers, and (5) grass carp (*Ctenopharyngodon idella*) grazing.

Benthos and Seston

The Tennessee River benthic fauna suffered as a result of impoundment and have been adversely affected by low DO concentrations from hypolimnetic dam discharges. Benthic fauna below most mainstream impoundments is typically rheophilic, including mussels, residual populations of snails, sponges, bryozoa, and insects. Isom (1971a, 1971b) prepared an annotated bibliography and has reviewed the significance and environmental effects on benthic invertebrates of the Tennessee River. Individual segment analyses are included in his report with more recent analyses by Wade (1985) for limited sections of the river. Phytoplankton, periphyton and zooplankton investigations have been sporadic and less than encompassing for the Tennessee River. Several reports have been prepared in association with steam-electric plants. Placke (1983) included phytoplankton standing crops and chlorophyll analyses in a trophic classification report; she concluded that the great majority of reservoirs was dominated by bluegreen algae. Similar results have been obtained from other reservoirs within the system.

Mollusks

Prior to impoundment, the Tennessee River system contained 100 species; it now contains approximately 80. In the early 1900's, mussels were harvested for their shells, which were used to make buttons. Early-1900 annual harvests amounted to approximately 580 t; peak harvests in the mid-1950's reached 10 400 t (Isom 1969); present harvest is approximately 640 t. The decline from peak harvests was caused by plastics supplanting natural material in the button industry; currently, mussel shells are used to provide nuclei in the cultured pearl industry. As a result of Isom's (1969) extensive survey of Tennessee Valley mussel populations and harvesting practices, mussel sanctuaries were established below all Cumberland and Tennessee River dams in Tennessee and Kentucky, and below TVA dams in Alabama; all three states also implemented harvest regulations. Jenkinson (1981) identified 12 molluscan species (11 bivalves, 1 gastropod) worthy of being federally listed as endangered, and another 25 species (24 bivalves, 1 gastropod) which were being adversely impacted through significant portions of their ranges.

Fisheries

Despite the interest shown in the Tennessee River and its tributary streams by early ichthyologists, among them Cope, Evermann, C. H. Gilbert, and Jordan (Shoup 1974), no clear picture of the piscine assemblage of the system existed prior to the commencement of TVA's activities. Moreover, except for an investigation late in TVA's dam-construction phase (Fitz 1968), no attention was given to the impacts of impoundment on the piscine community; this tends to be the worldwide rule, rather than the exception (Petts 1984). Prior to the development of impoundments, the Tennessee River system probably supported a typical, temperate warmwater stream fauna, with ictalurids, centrarchids and large catostomids (*Ictiobus*) dominating the lower reaches and cyprinids and small percids (darters) being more prevalent in the upper reaches and lower-order streams. Impoundment resulted in the loss of those riverine species not able to adapt to more lacustrine conditions. The brunt of the impact was undoubtedly borne by small cyprinids and percids; of the 12 species lost after impoundment of Melton Hill Reservoir, 7 were of this group (Fitz 1968).

The expansion of lacustrine habitat resulted in increases in numbers and biomass of most centrarchids, ictalurids, and clupeid forage species (*Dorosoma*). For some species, expansion of populations following impoundment was apparently temporary, as the initial advantages of increased space and food were overcome by the disruption of historic hydrologic regimes and loss of riverine habitat necessary for reproduction. Hackney and Holbrook (1978) speculated that walleye (*Stizostedion vitreum vitreum*) were thus affected, and based on recent research (Pasch et al. 1980; Wallus 1986) it appears that paddlefish (*Polyodon spathula*) were similarly impacted.

With respect to the piscine community, mainstream reservoirs support a greater total biomass than do tributary reservoirs (average, 380 $\text{kg} \cdot \text{ha}^{-1}$ vs. 283), contain more species, and have a higher and less-variable ratio of prey species to predators (Table 4).

Mean total standing stocks in Tennessee River reservoirs range from 85 to 915 $\text{kg} \cdot \text{ha}^{-1}$ (Table 5), as estimated by sampling small embayments (coves) with rotenone (Hall 1974). Mainstream reservoir stocks generally are dominated by centrarchids (*Lepomis* spp. and *Micropterus* spp.) among gamefish species; cyprinids (*Cyprinus carpio*), catostomids (*Ictiobus* spp. and *Minytrema melanops*), ictalurids (*Ictalurus* spp.) and sciaenids (*Aplodinotus*) among the rough or commercial species; and clupeids (*Dorosoma* spp.) among forage species. Storage reservoir stocks are similar in composition, except that white bass (*Morone chrysops*), percids (*Stizostedion* spp.) and crappie (*Pomoxis* spp.) are somewhat more important components of the standing stock and *Aplodinotus grunniens* and *Dorosoma* spp. less so.

Annual estimates of standing stocks are highly variable among reservoirs (Table 5). Most of the annual variation is caused by large annual fluctuations in biomass of gizzard and threadfin shad (*Dorosoma cepedianum* and *D. petenense*). In 5 of the 14 years represented in the Cherokee Reservoir data, *Dorosoma* stocks exceeded 1 000 $\text{kg} \cdot \text{ha}^{-1}$ and over 16 years accounted for more than 70 % of total standing stock.

In an analysis of fish species associations of the Tennessee River impoundments, Barr (1978) recorded 117 species belonging to 22 families from 708 cove-rotenone samples; of these, 82 species belonging to 15 families occurred in 10 % or more of the samples in one or more reservoirs. Starnes and Etnier (1986) report a total of 225 species, of which 216 are native and 9 are naturalized species. Barr (1978) identified three distinct species associations within Tennessee and Cumberland River impoundments; these associations correlate closely with storage ratio, elevation, and other environmental factors which describe the basic differences between lowland, mainstream and upland, storage reservoirs (McDonough and Barr 1977).

Factors Influencing Fish Production

Two groups of factors may influence the development of standing stock biomass: (1) the physical and chemical attributes of the reservoirs, e.g., morphometry and nutrients, and (2) operational characteristics and other anthropogenic activities.

Hickman and Hevel (1986) found significant inverse correlations between (1) numbers of young-of-the-year fish and (2) growth of age-1 largemouth bass in Melton Hill Reservoir and the volume of hypolimnetic discharge from Norris Dam. They concluded that the principal factor was reduced water temperature during the period of spawning and early growth. Simple linear regression analyses of fish standing stocks on physical and chemical variables (Table 6) indicate that P is the most important variable among those inspected, i.e., those in Tables 1 and 3, plus chlorophyll *a* and area less than 1.7 m depth from Placke (1983).

Regressions involving MEI yielded values well within the range reported by Carline (1986); however, the analysis was limited by the lack of adequate suspended solids data for mainstream reservoirs. Following Ryder's (1982) observations, a P-based MEI (PMEI) was used (Fig. 3 and 4), where PMEI = net P load ($\text{kg} \cdot \text{d}^{-1}$) /mean depth, m. The relationship between PMEI and fish biomass was consistently stronger than for MEI or NMEI in tributary reser-

TABLE 5. Means and standard errors (SE) of fish standing stock biomass (kg• ha^{-1}) for Tennessee River mainstream reservoirs and eight tributary reservoirs. N is number of annual estimates; each annual estimate consists of sampling two or more coves. Symbols for fish families and genera are defined below.

			Fish families and genera[a]									
	N	Total	Pc	Le	Mi	Po	Pe	Cl	Ca	Cy	Ic	Sc
					Mainstream							
Kentucky	9	380	0.9	26	7.4	3.0	1.1	181	52	41	9.1	41
	SE	30	0.2	4	1.1	1.0	0.2	16	12	9	0.6	8
Pickwick	9	365	1.6	34	9.7	2.2	1.8	186	56	29	20	18
	SE	40	0.3	5	0.9	0.7	0.3	46	9	7	4	3
Wilson	4	447	0.6	67	14	0.1	0.6	158	44	18	88	53
	SE	125	0.1	10	3	*	0.4	123	11	13	47	20
Wheeler	17	711	2.4	89	17	2.1	0.8	381	116	24	21	50
	SE	78	1.0	8	8	0.7	0.2	45	8	5	3	7
Guntersville	10	298	2.5	65	10	2.2	0.4	144	25	12	8.1	40
	SE	23	0.7	7	0.9	0.4	0.1	23	10	3	2	8
Nickajack	5	249	1.4	85	11	0.7	0.2	94	6.4	23	8.2	11
	SE	23	0.3	12	2	0.3	*	11	4	11	2.5	4
Chickamauga	16	331	2.3	44	11	2.4	1.3	165	31	27	14	26
	SE	24	0.7	4	0.8	0.5	0.2	22	6	4	3	2
Watts Bar	7	300	2.0	23	7.7	2.9	1.5	116	44	65	8.8	27
	SE	42	0.5	4	1.0	1.9	0.4	29	7	16	1.8	3
Fort Loudoun	4	336	1.8	34	8.7	7.2	0.5	170	27	54	12	21
	SE	36	0.5	9	1.8	1.9	0.2	31	3	10	4	4
					Tributary							
Chatuge	2	86	1.3	32	9.6	2.3	5.0	22	0.5	11	2.4	—
	SE	—	—	—	—	—	—	—	—	—	—	
Cherokee	16	924	5.0	52	20	6.2	—	707	34	76	21	11
	SE	128	1.2	11	3	1.9		125	5	15	4	2
Douglas	4	309	0.6	16	14	33	5.4	107	50	42	20	19
	SE	101	0.2	5	4	9	2.6	78	15	13	3	12
Fontana	4	106	1.5	22	7.1	11	6.1	28	7.3	13	8.2	—
	SE	22	0.4	7	1.1	5	3.2	7	2.9	7	1.6	
Norris	15	190	3.0	15	8.8	2.0	2.3	129	2.6	16	5.1	5.0
	SE	12	0.8	2	0.8	1.1	0.9	8	0.5	3	0.6	0.8
South Holston	7	324	1.5	39	10	14	—	163	11	71	9.0	—
	SE	47	0.4	5	0.9	4		31	4	22	1.5	
Tims Ford	3	175	0.7	28	5.2	0.7	0.2	62	23	40	6.8	3.2
	SE	54	0.5	22	1.4	0.7	0.1	21	21	22	6.1	2.5
Watauga	9	153	—	26	6.1	5.0	3.5	71	35	15	6.0	1.3
	SE	19	—	4	0.8	1.6	1.4	14	4	7	2.0	0.3

[a] Pc-Percichthyidae; Le-*Lepomis*; Mi-*Micropterus*; Po-*Pomoxis*; Pe-Percidae Cl-Clupeidae; Ca-Catostomidae; Cy-Cyprinidae; Ic-Ictaluridae; Sc-Sciaenidae

*SE less than 0.05; SE's for Chatuge (N=2) not calculated.

voirs; all R^2 exceeded 0.35. The surprising outcome was the difference in the sign of the relationship for the two sets of reservoirs (Fig. 3). For mainstream reservoirs, the negative relationship is driven by Wheeler Reservoir, which has the highest total standing stock and most negative PMEI.

The apparent difference in response of the two data sets is due to (1) the physical association among reservoirs, (2) differences in hydraulic characteristics, and (3) significant differences in allochthonous influences. The eight tributary reservoirs analyzed (Hiwassee lacks data on fish stocks) are essentially independent, whereas the nine mainstream reservoirs are in a cascading series (Fig. 1). Placke (1983) concluded that chlorophyll production in tributary reservoirs was strongly correlated with P and N concentrations, while in mainstream reservoirs, light and hydraulics (higher turbidity, significantly shorter retention times) were the principal limiting factors. Moreover, it is obvious that the calculation of net P load in mainstream reservoirs does not accurately reflect P dynamics within these reservoirs. Mainstream reservoirs obviously do not generate P, as the negative net loads would imply; there are important sources of P which are not fully accounted for by inflow-outflow measurements, e.g., intensive and highly fertilized agriculture, industrial and municipal discharges, and large tributary streams — all of these sources are appreciably more important in the case of mainstream reservoirs. The absolute value of net P loadings, and hence PMEI, is probably an imperfect estimate of load; utilizing absolute values changes the sign of the PMEI — standing stock relationship for mainstream reservoirs and yields a significant regression with R^2 = 0.61.

Cherokee Reservoir, classified as a tributary reservoir, is an extreme example of excessive nutrient input on the piscine community. The Holston River upstream of the reservoir proper is subjected to N and P loads estimated at 14 700 and 1 145 kg• d^{-1}, respectively, and total dissolved

TABLE 6. Results of simple linear regression analysis ($Y = a + bX$) of fish standing stock biomass versus physical and chemical characteristics of reservoirs. Entries limited to those with R^2 exceeding 0.40.

Regression	*a*	*b*	R^2
Mainstream			
Total — PMEI	347	− 0.37	0.65
Clupeid — PMEI	156	− 0.24	0.75
Catostomid — PMEI	36.9	− 0.09	0.69
Micropterus — PMEI	11.4	− 0.002	0.65
Total — Net P load	353	− 67.4	0.52
Clupeid — Net P load	159	− 46.3	0.67
Catostomid — Net P load	38.3	− 16.2	0.58
Micropterus— Net N load	11.4	− 0.33	0.71
Clupeid — % area < 1.7 m depth	35.8	8.45	0.49
Percichthyid — % area < 1.7 m	0.62	0.07	0.46
Tributary			
Total — PMEI	107	4.02	0.90
Percichthyid — PMEI	1.14	0.02	0.48
Micropterus — PMEI	6.9	0.07	0.93
Clupeid — PMEI	21.2	3.18	0.83
Cyprinid — PMEI	22.6	0.29	0.51
Ictalurid — PMEI	5.5	0.10	0.83
Percichthyid — NMEI	1.44	0.006	0.86
Clupeid — NMEI	107	55.4	0.52
Total — Net P load	62.8	481	0.91
Percichthyid — Net P load	0.88	2.07	0.55
Lepomis — Net P load	21.9	14.8	0.42
Micropterus — Net P load	6.34	8.21	0.84
Clupeid — Net P load	− 15.3	385	0.85
Cyprinid — Net P load	17.6	39.1	0.64
Ictalurid — Net P load	4.89	10.8	0.71
Percichthyid — Net N load	1.21	0.58	0.79
Pomoxis — Chlorophyll *a*	2.49	3.37	0.47
Catostomid — Chlorophyll *a*	− 10.8	6.11	0.55
Cyprinid — Chlorophyll *a*	− 6.0	8.14	0.45
Ictalurid — Chlorophyll *a*	− 5.04	2.91	0.84

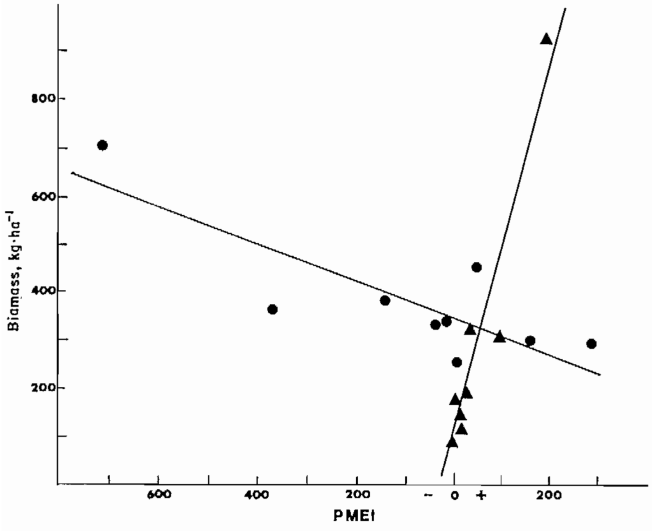

FIG. 3. Total standing stock biomass (kg•ha^{-1}) versus P-based morphoedaphic index (PMEI) for mainstream (circles) and tributary (triangles) reservoirs.

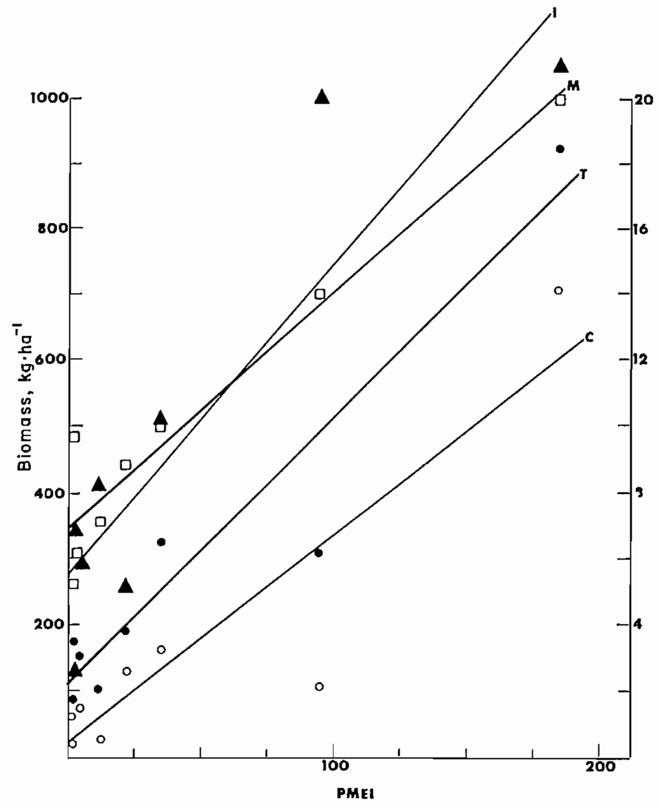

FIG. 4. Standing stock biomass versus PMEI. Closed circles = clupeids (C); open circles = total biomass (T); squares = ictalurids (I); triangles = *Micropterus* (M). Scale on left axis: total and clupeids; right: ictalurids and *Micropterus*.

organic C, measured by 5-day BOD, is 10 024 kg• d^{-1} (Young and Dennis 1983). Production of aquatic macrophytes, principally *Potamogeton pectinatus* and *Vallisneria americana*, amounts to 25.2 t • ha^{-1} • yr^{-1}; the resultant annual N and P contribution to Cherokee from this source alone is 196 and 21 t, respectively (Young and Dennis 1983). The effects are those of classic eutrophication. Cherokee yields the highest mean standing stock and the greatest percentage of clupeid forage fish (Table 5); the epilimnion is very shallow and the large hypolimnion is oxygen-deficient for significant periods — discharges from Cherokee Dam average less than 1 mg • L^{-1} for 30 days and less than 5 mg • L^{-1} (the State of Tennessee criterion) for 131 days annually.

Fisheries Management

Early management practices were organized around the belief that reservoirs would not support self-sustaining fish populations (Chance et al. 1975). Accordingly, initial efforts emphasized fish culture and "fish rescue" operations, wherein fish were removed from pools formed during reservoir drawdown and transplanted either to that, or another, reservoir. Early research and management efforts were devoted to determining the self-sustaining nature of important game-fish species, documenting distribution, harvest, and life history characteristics, and developing management regulations (e.g., Eschmeyer and Manges 1945; Dendy 1945).

Species introductions were, and remain, a significant management activity. Early (1936–50) introductions were, with the exception of rainbow trout, brook trout (*Salvelinus fontinalis*), and lake trout (*S. namaycush*), transplants of indigenous species (Barr 1978; Starnes and Hackney unpublished data). More recent introductions have included a greater number of non-native species or stocks, e.g., striped bass (*Morone saxatilis*), Ohio muskellunge (*Esox masquinongy*), northern pike (*E. lucius*), brown trout (*Salmo trutta*), cutthroat trout (*S. clarki*), Ohrid trout (*S.* letnica), kokanee (*Oncorhynchus nerka*), cisco (*Coregonus artedii*), rainbow smelt (*Osmerus mordax*), and alewife (*Alosa pseudoharengus*) (Starnes and Hackney unpublished data). The majority of these introductions (salmonids, esocids and striped bass) were made with the intent of supplementing native game-fish stocks; cisco, smelt and alewife were introduced to provide additional prey. With the exception of brown and rainbow trout, salmonid introductions have apparently been unsuccessful, as has the rainbow smelt experiment. Striped bass introductions have proven successful in most reservoirs, but as with the salmonids, apparently will not develop self-sustaining populations. Perhaps the most recent addition is the sauger × walleye hybrid (saugeye), which was introduced into Cherokee Reservoir in 1982 to replace extirpated native populations. Preliminary results indicate significant success in terms of growth and harvest. The alewife, introduced into Watauga Reservoir in eastern Tennessee in 1976, has extended its range downstream into Cherokee Reservoir and may spread throughout the system.

One accidental introduction has been documented. Yellow perch (*Perca flavescens*) apparently were introduced accidentally during walleye and sauger stocking activities in Chatuge Reservoir in the 1950's (Timmons 1975); by 1978, they had invaded the mainstream Tennessee (Chickamauga Reservoir) via the Hiwassee River and were reported both upstream as far as Melton Hill Reservoir and downstream as far as Wheeler Reservoir (Hackney and Holbrook 1978).

During the period of rapid expansion of impounded waters, fisheries resources also expanded and thus exceeded demand; from 1935 to 1945, the total surface area of impounded water in the Tennessee Valley increased by a factor of 18.6, while the regional population increased by a factor of 1.1 (Barr 1978). During this period, and, in fact, well into the 1970's, fishery managers appear to have been concerned largely with providing access for anglers, promoting greater fishing pressure (and hence, more fishing-license sales, which determined their budgets) and occasionally introducing an "exotic" or "trophy" species to heighten angler interest. The strategy apparently has worked: in 1933, annual sport fish harvest was 56.8 t; currently it is estimated at 770 t. No comprehensive nor consistent efforts are made in the Valley states to estimate sport fish harvest; thus analysis of trends is impossible, although some fisheries biologists suspect that the current estimate of 770 t may represent a slight decrease from peak harvests in the mid-1970's. Commercial harvest, which is principally from mainstream reservoirs, has increased from 2 240 t in 1960 and 2 910 t in 1970 to the present (1984) estimate of about 4 200 t.

Beyond the classical management practices, two approaches involving habitat management were developed in the 1970's. Prior to this time, as a means of reducing potential habitat for malarial-mosquito reproduction, reservoirs in the Tennessee Valley were cleared of all timber and underbrush before closure. In the construction of Normandy Reservoir (closed in 1976), several areas identified as potentially good fish habitat were not cleared. These areas were marked on fishing maps and have proven popular angling areas. Fish attractors, consisting of brush piles or groups of concrete blocks, were installed in several reservoirs during the late 1970's to provide both shelter and a means of concentrating sport fish. These have proven popular, especially when combined with improved shoreline-access facilities.

Unfortunately, another attempt at habitat improvement has yielded mixed blessings. Eurasian watermilfoil, now the principal "nuisance" aquatic macrophyte and the object of intensive control efforts, apparently was originally introduced into Guntersville Reservoir by fishermen seeking to provide more cover for largemouth bass.

Fisheries Research

Increased concern over environmental quality, as publicly and nationally expressed in the *National Environmental Policy Act* of 1969, the *Federal Water Pollution Control Act Amendments* of 1972 (now know as the *Clean Water Act*), and the *Endangered Species Act* of 1973, significantly increased both investigations and assessments of aquatic resources, including fisheries (e.g., Hackney and Webb 1978; Voigtlander 1980, 1981; Waddle et al. 1980; Wrenn 1980) and public awareness of the existence and status of these resources. It would appear that the information generated, as well as the techniques and philosophies of the assessment and mitigation of environmental impacts could be translated into management practices. However, the "cross-over" from environmental research to fisheries management has proven minimal thus far. Interest in the impacts of a new form of fishing, bass-fishing tournaments (Holbrook 1975) led to changes in tournament conduct, e.g., minimum-length requirements and emphasis on returning fish alive to the lake or reservoir. Investigations on the biology of paddlefish, stimulated by questions of power-plant impacts, brought out instances of illegal harvest of paddlefish (for caviar) during the spawning season. Upon being notified, the State of Tennessee took regulatory and enforcement actions to halt the illegal practices.

Endangered species issues have arisen in conjunction with two major TVA projects. Construction and closure of Tellico Dam on the Little Tennessee River threatened the existence of the snail darter (*Percina tanasi*). Investigations of the life history of the species (Hickman and Fitz 1978) led to a transplanting program which resulted in the establishment of a self-sustaining population (Hickman 1981). Construction of Columbia Dam on the Duck River threatens two endangered freshwater mussels (*Conradilla caelata* and *Quadrula intermedia*). The conservation program (Jenkinson 1982, 1983), which has applicability to the entire Cumberlandian mollusk fauna, has inspired the development of *in vitro* culture techniques (Isom and Hudson 1982; Isom 1983). The ultimate success of the program is as yet unproven and the future of the Columbia Dam project is uncertain.

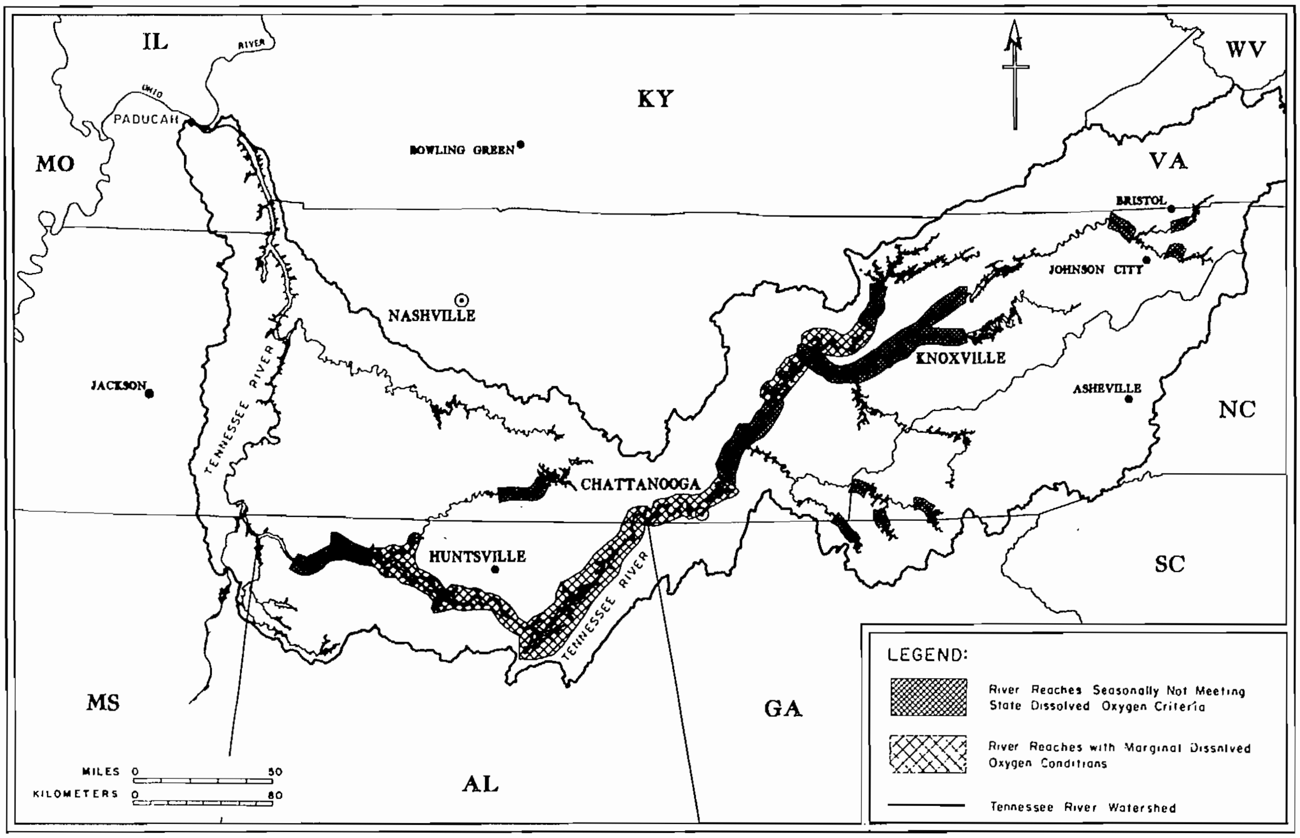

FIG. 5. Tailwaters and reservoir areas that seasonally do not meet state dissolved oxygen criteria as a result of hypolimnetic hydropower discharges. Marginal areas are those in which waste assimilative capacity has been reduced.

The Outlook for Fisheries

Early in its existence, TVA adopted a strategy of low-cost electrical generation and industrial development as the best means of improving the depressed economy of the Valley. This strategy, still in force, will be the focus of resource conflicts involving the allocation of water, and as a result, fisheries resources. Management of the reservoir system, except during emergencies (flood danger, drought) is dominated by the needs of hydroelectric generation, which produces the cheapest power. Hydrogeneration, which creates hypolimnetic discharges, is the principal cause of reduced DO in tailwaters and downstream reservoirs (Fig. 5); low-DO problems are exacerbated by the demands placed on waste assimilative capacity by industries and wastewater treatment facilities. Little progress has been made in controlling non-point source pollution from agricultural, mining, and urban runoff or in protecting groundwater from contamination. Projections of industrial development indicate that principal growth will be in the areas of rubber and plastics, fabricated metals, chemicals, and electronics and electrical machinery — many such operations are sources of toxic discharges. Given the continuing public and political pressure to maintain low electrical rates and foster industrial development, the situation is unlikely to change.

The Tennessee Valley watershed includes portions of seven states. These states exert control over natural resources management (e.g., fisheries management) and with few exceptions, have assumed legal authority for environmental regulation and protection. However, no comprehensive, coordinated attempt at managing aquatic resources or protecting and enhancing environmental quality has been made. States have differing fish management priorities and strategies, and promulgate differing environmental standards. Moreover, priorities for natural resources management are relatively low; in 1980, combined expenditures by Alabama, Kentucky and Tennessee for fish management were less than for nine other states, and approximately equalled those by Wyoming, despite the obvious differences in water area and population. TVA, with its enabling legislation mandating a regional resource-development role, but unable to undertake overt management (e.g., stocking fish; establishing environmental standards) except on its own lands, has sought to influence resource management by performing planning and coordination functions. Planning activities range from reservoir land-use plans (where TVA controls considerable shoreline land areas) to reservoir water quality and fisheries management plans. These plans, which describe and quantify the resources in question and recommend needed actions, are presented to State agencies for their consideration, together with the identification of activities or services that TVA is willing to perform. The planning processes, while imperfect, generally have proven more successful than has the implementation of the recommendations, owing to fragmentation of efforts within TVA and to differing perceptions, differing priorities, and inadequate funding on the part of the states.

That the Tennessee River system, for the most part, still supports a reasonably well-balanced fish community capable of supporting high angling and moderate commercial yields, is perhaps less a tribute to man's resource-management capabilities than to the resilience of most of the species in question. The critical question remains: how far can that resilience be stretched?

Acknowledgments

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References

BARR, W. C. 1978. The use of cove-rotenone studies for fisheries management in southern reservoirs. Ph.D. Dissertation, Univ. Tennessee, Knoxville, TN. 184 p.

BOHAC, C. E., R. M. SHANE, E. D. HARSHBARGER, AND H. M. GORANFLO. 1986. Recent progress on improving reservoir releases, p. 187–190. *In* G. Redfield, J. M. Taggart, and L. M. Moore [ed.] Lake and Reservoir Management, Vol. II. N. Am. Lake Manage. Soc., Washington, DC.

BURNS, E. R., A. L. BATES, AND D. H. WEBB. 1984. Aquatic weed control program: seasonal workplan and current status. Tenn. Valley Auth. Rep. TVA/ONRED/AWR-84/15. 56 p.

CARLINE, R. F. 1986. Indices as predictors of fish community traits, p. 46–56. *In* G. E. Hall and M. J. Van Den Avyle [ed.] Reservoir fisheries management — strategies for the 80's. Southern Division, American Fisheries Society. Bethesda, MD.

CHANCE, C. J., A. O. SMITH, J. A. HOLBROOK II, AND R. B. FITZ. 1975. Norris Reservoir: a case history in fish management, p. 399–407. *In* H. Clepper [ed.] Black bass biology and management. Sport Fishing Institute, Washington, DC.

DAVIS, J. L., C. E. BOHAC, E. D. HARSHBARGER, AND R. M. SHANE. 1983. Experience with reservoir release aeration and flow improvement. Proc. Waterpower 83. Am. Soc. Civ. Eng: 1326–1335.

DENDY, J. S. 1945. Fish distribution, Norris Reservoir, Tennessee, 1943. II. Depth distribution of fish in relation to environmental factors, Norris Reservoir. J. Tenn. Acad. Sci. 20: 114–135.

ESCHMEYER, R. W., AND D. E. MANGES. 1945. Effect of a year-round open season on fishing in Norris Reservoir. J. Tenn. Acad. Sci. 20: 20–34.

FITZ, R. B. 1968. Fish habitat and population changes resulting from impoundment of the Clinch River by Melton Hill Dam. J. Tenn. Acad. Sci. 43: 7–15.

HACKNEY, P. A., AND J. A. HOLBROOK II. 1978. Sauger, walleye, and yellow perch in the southeastern United States, p. 74–81. *In* R. L. Kendall [ed.] Selected coolwater fishes of North America. Am. Fish. Soc. Spec. Publ. 11. Washington, DC.

HACKNEY, P. A., AND J. C. WEBB. 1978. A method for determining growth and mortality rates of ichthyoplankton, p. 115–124. *In* L. D. Jensen [ed.] Fourth national workshop on entrainment and impingement. Ecological Analysts, Inc., Sparks, MD.

HALL, G. E. 1974. Sampling resevoir fish populations with rotenone. FAO Symposium on methodology for the survey, monitoring, and appraisal of fisheries resources in lakes and large rivers. Aviemore, Scotland, May 2–4, 1974. 14 p.

HICKMAN, G. D. 1981. Is the snail darter transplant a success? p. 338–344. *In* L. A. Krumholz [ed.] The warmwater streams symposium. Southern Division, American Fisheries Society, Bethesda, MD.

HICKMAN, G. D., AND R. B. FITZ. 1978. A report on the ecology and conservation of the snail darter (*Percina tanasi* Etnier) 1975–1977. Tenn. Valley Auth. Forest., Fish. Wildl. Tech. Note B28, Norris, TN. 130 p.

HICKMAN, G. D., AND K. W. HEVEL. 1986. Effect of a hypolimnetic discharge on reproductive success and growth of warmwater fish in a downstream impoundment, p. 286–293. *In* G. E. Hall and M. Van Den Avyle [ed.] Reservoir fisheries management — strategies for the 80's. Southern Division, American Fisheries Society, Bethesda, MD.

HIGGINS, J. M., W. L. POPPE, AND M. L. IWANSKI. 1980. Eutrophication analysis of TVA reservoirs, p. 404–412. *In* H. G. Stefan [ed.] Surface water impoundments. Vol. 1. Am. Soc. Civil Eng., New York, NY.

HOLBROOK, J. A. II. 1975. Bass fishing tournaments, p. 408–415. *In* H. Clepper [ed.] Black bass biology and management. Sport Fishing Institute, Washington, DC.

ISOM, B. G. 1969. The mussel resource of the Tennessee River. Malacologia 7: 397–425.

1971a. Aquatic invertebrates of the Tennessee Valley region. A partially annotated bibliography. Tenn. Valley Auth. 39 p.

1971b. Effects of storage and mainstream reservoirs on benthic macroinvertebrates in the Tennessee Valley, p. 17–191. *In* G. E. Hall [ed.] Reservoir fisheries and limnology. Am. Fish. Soc. Spec. Pub. No. 8.

1983. Potential uses of *in vitro* culture of freswater mussel glochidia for conservation, p. 42–45 *In* A. C. Miller [compiler] Report of freshwater mussels workshop 26–27 October 1982. U.S. Army Eng. Waterways Exp. Station, Vicksburg, MS.

ISOM, B. G., AND R. G. HUDSON. 1982. *In vitro* culture of parasitic freshwater mussel glochidia. Nautilus 96: 147–151.

JENKINSON, J. J. 1981. Endangered or threatened aquatic mollusks of the Tennessee River system. Bull. Am. Malacolog. Union 1981: 43–45.

1982. Cumberlandian mollusk conservation program, p. 95–103. *In* A. C. Miller [compiler] Report of freshwater mollusks workshop, 19–20 May 1981. U.S. Army Eng. Waterways Exp. Station, Vicksburg, MS.

1983. Status report on the Tennessee Valley Authority Cumberlandian mollusk conservation program, p. 79–83. *In* A. C. Miller [compiler] Report of freshwater mussels workshop, 26–27 October 1982. U.S. Army Eng. Waterways Exp. Station, Vicksburg, MS.

LESESNE, E. D. 1974. The water control system and changes in multipurpose use, p. 427–446. *In* H. Knop [ed.] The Tennessee Valley Authority experience Vol. 1. Int. Inst. Applied Systems Analysis, Laxenburg, Austria.

MCCARTHY, D. M., AND C. W. VOIGTLANDER [ed.]. 1983. The first fifty years: changed land, changed lives — state-of-the-environment in the Tennessee Valley. TVA, Knoxville, TN. 212 p.

MCDONOUGH, T. A., AND W. C. BARR. 1977. An analysis of fish associations in Tennessee and Cumberland drainage impoundments. Proc. Annual Conf. S.E. Assoc. Fish and Wildlife Agencies 31: 555–563.

PASCH, R. W., P. A. HACKNEY, AND J. A. HOLBROOK II. 1980. Ecology of paddlefish in Old Hickory Reservoir, Tennessee, with emphasis on first-year life history. Trans. Am. Fish. Soc. 109: 157–167.

PETTS, G. E. 1984. Impounded rivers. Perspectives for ecological management. John Wiley and Sons, New York, NY. 326 p.

PLACKE, J. F. 1983. Trophic status evaluation of TVA reservoirs.

Tenn Valley Auth. Tech. Rep. TVA/ONR/WR-83/7. Chattanooga, TN. 163 p.

POPPE, W. L. 1984. Artificial destratification: summary of results obtained from Normandy Reservoir. Tenn. Valley Auth. Tech. Rep. TVA/ONRED/AWR-84/32. Chattanooga, TN. 31 p.

RYDER, R. A. 1982. The morphoedaphic index — use, abuse and fundamental concepts. Trans. Am. Fish. Soc. 111:154–164.

SHOUP, C. S. 1974. A bibliography of the zoology of Tennessee and the Tennessee Valley Region. U.S. Atomic Energy Comm. Rep. NP-19905. Oak Ridge, TN. 251 p.

STARNES, W. C., AND D. A. ETNIER. 1986. Drainage evolution and fish biogeography of the Tennessee and Cumberland rivers drainage realm, p. 325–361. *In* C. H. Hocutt and E. O. Wiley [ed.] The zoogeography of North American freshwater fishes. John Wiley & Sons, New York, NY.

TDHE (TENNESSEE DEPARTMENT OF HEALTH AND ENVIRONMENT). 1986. Status of water quality in Tennessee. 1986. Section 305(b) report. Division of Water Management, Nashville, TN. 138 p.

TENNESSEE VALLEY AUTHORITY. 1936. The unified development of the Tennessee River system. Rep. to U.S. Congress, March 31, 1936. 105 p.

TIMMONS, T. J. 1975. Range extension of the yellow perch, (*Perca flavescens* (Mitchill)), in Tennessee. J. Tenn. Acad. Sci. 50: 101–102.

VOIGTLANDER, C. W. 1980. Effects of cooling water intakes on fish populations: entrainment and impingement, p. 60–70. *In* Environmental effects of cooling systems. Tech. Rep. Ser. No. 202. International Atomic Energy Agency, Vienna, Austria. 196 p.

1981. If you can't measure an impact, there probably isn't an impact, p. 3–11. *In* L. D. Jensen [ed.] Issues associated with impact assessment. Proc. Fifth Ann. Nat'l. Workshop on Entrainment and Impingement. Ecological Analysts, Inc., Sparks, MD.

WADDLE, H. R., C. C. COUTANT, AND J. L. WILSON. 1980. Summer habitat selection by striped bass, *Morone saxatilis*, in Cherokee Reservoir, 1977. Environmental Sciences Div. Publ. No. 1360. Oak Ridge National Laboratory, Oak Ridge, TN. 195 p.

WADE, D. C. 1985. Preoperational assessment of water quality and biological resources of Guntersville Reservoir in the vicinity of Bellefonte Nuclear Plant, 1974–1984. Tenn. Valley Auth. Rep. TVA/ONRED/WRF-86/1, Knoxville, TN. 469 p.

WALLUS, R. 1986. Paddlefish reproduction in the Cumberland and Tennessee River systems. Trans. Am. Fish. Soc. 115: 424–428.

WRENN, W. B. 1980. Effects of elevated temperature on growth and survival of smallmouth bass. Trans. Am. Fish. Soc. 109: 617–625.

YOUNG, R. C., AND W. M. DENNIS. 1983. Productivity of the aquatic macrophyte community of the Holston River: implications to hypolimnetic oxygen depletion of Cherokee Reservoir. Tenn. Valley Auth. Div. Air and Water Resources. 34 p.

Amazon Fisheries: Assessment Methods, Current Status and Management Options

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Abstract

BAYLEY, P. B., AND M. PETRERE JR. 1989. Amazon fisheries: assessment methods, current status and management options, p. 385–398. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

A variety of food fisheries exist which are distinguished more by socioeconomic than national differences. Of the 199 000 t annual yield in the basin, 61% derives from local market/subsistence fisheries for which an estimation method is described. The species composition of these fisheries is very different from commercial fisheries, which specialize on a few large species except near the cities. Floodplain areas were estimated, and on the basis of comparative data from other tropical areas, the total yield could be quadrupled or more, depending on the type and quantity of effort and the maintenance of the hydrological regime. With increasing effort near the cities, stocks of some large species are declining, but the diversity of the catch is increasing as smaller species become accepted in the market. This trend will increase with further effort, but extinction of fish species is considered very unlikely if the quality of the environment is maintained. A variety of management options are discussed in the light of socioeconomic differences between the fisheries. It is recommended that high yield, multispecies fisheries be allowed to expand near major, populated areas but restrictions on commercial fisheries be placed on selected, distant river–floodplain areas in order to maintain a higher productivity of larger species and to preserve unique ecosystems.

Résumé

BAYLEY, P. B., AND M. PETRERE JR. 1989. Amazon fisheries: assessment methods, current status, and management options, p. 385–398. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Il existe diverses pêches de subsistance qui se distinguent davantage par des différences socio-économiques que par des différences au niveau national. Des 199 000 tonnes de poisson capturé annuellement dans le bassin versant, 61 % proviennent de marchés locaux et de pêches de subsistance pour lesquels on présente une méthode d'estimation du rendement annuel. La composition des espèces capturées dans le cadre de ces pêches est très différente de celle observée dans les pêches commerciales centrées sur quelques espèces de gros poissons sauf près des villes. On a déterminé la superficie des plaines inondables et d'après une comparaison avec des données sur d'autres régions tropicales, on a calculé que le rendement total pourrait être quadruplé et même davantage selon le type et le niveau d'effort déployé et la permanence du régime hydrologique. Un accroissement de l'effort déployé près des villes entraîne un déclin des effectifs de certaines espèces de gros poissons mais la diversité des prises augmente étant donné que les espèces de petits poissons reçoivent de plus en plus la faveur des consommateurs. Même si cette tendance augmentera avec l'effort déployé, il est peu probable que les espèces visées disparaîtront si la qualité de l'environnement est maintenue. On examine diverses mesures de gestion à la lumière des différences socio-économiques entre les pêches. On recommande le développement des pêches polyvalentes à rendement élevé près des principales zones peuplées; par contre, les pêches commerciales devraient être limitées dans certaines régions éloignées de plaines inondables afin de maintenir un niveau plus élevé de productivité des espèces de gros poissons et de protéger ces écosystèmes uniques.

The authors describe the fish ecology of the Amazon basin (Fig. 1) and the various food fisheries existing since the mid 1970's when reliable data were first collected. Aspects of animal life histories are mentioned only when they pertain to the understanding of extant or potential fisheries. Historical fisheries are mentioned in Verissimo (1895), Smith (1981), Goulding (1983), and Junk (1984a). Bayley (1988) describes the environment and the importance of various sources of primary production leading to fish production. This paper discusses the immediate needs of fishery management assuming that environmental features maintaining fish productivity are preserved.

Ornamental fisheries are very localized and their impact is largely unknown. However, intensive fishing has caused

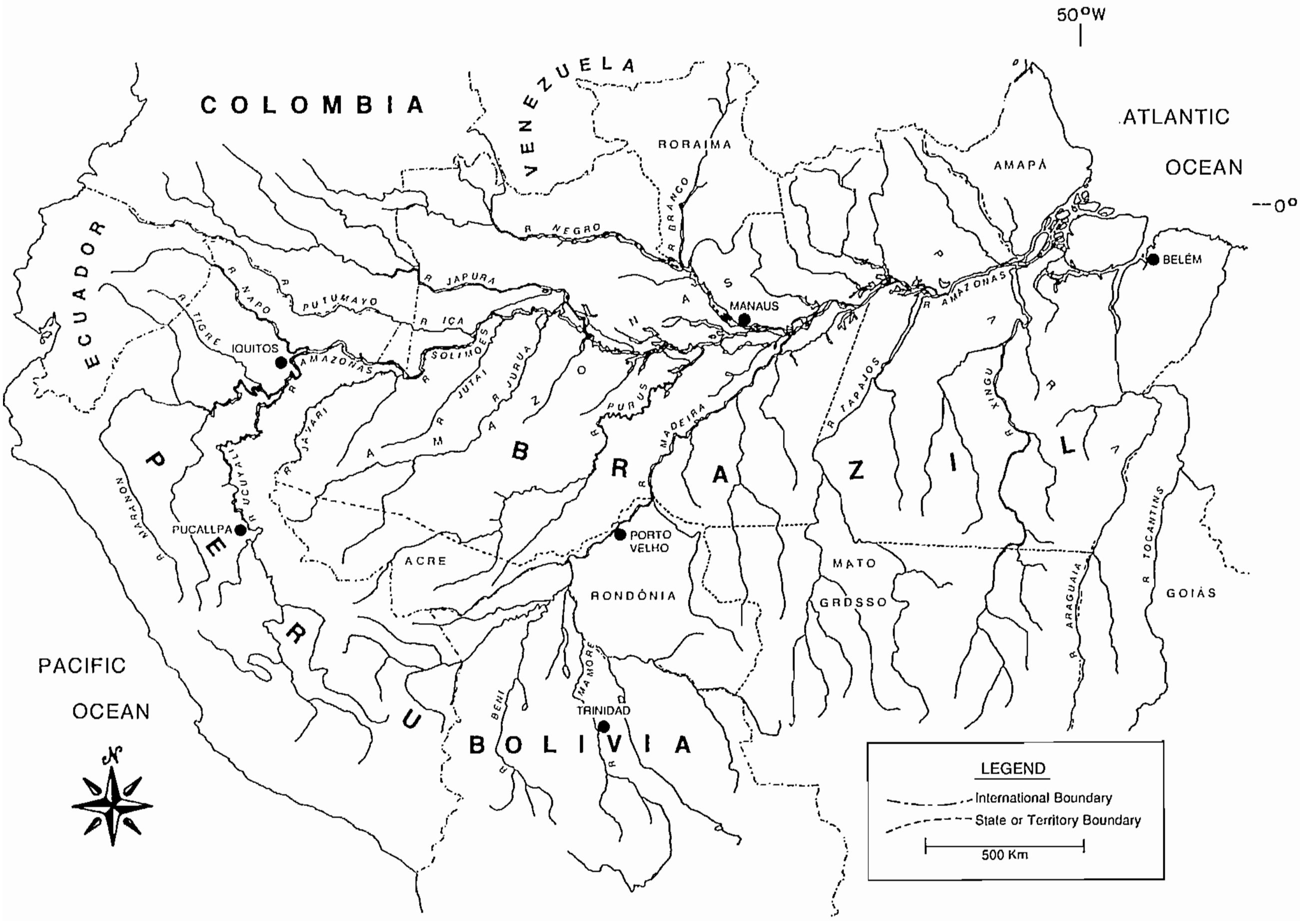

FIG. 1. Amazon basin with major rivers and political boundaries.

commercial extinction of discus, *Symphysodon* spp. in the lower R. Negro and the cardinal, *Paracheirodon axelrodi* in the middle R. Negro region (M. Goulding, pers. comm.). Species lists and export data are presented in Hanek (1982) and Junk (1984a). In the few areas where sport fishing is practised its influence is minor compared with food fisheries. The impact of ornamental or sport harvests in terms of energy or economics on the scale of the subsystems discussed in this paper is negligible.

Aquaculture is at an experimental stage in various parts of the basin, but its future is uncertain. Different views of its future have been discussed (Goulding 1979; Pedini 1981; Bayley 1984; Junk 1984a) and are not elaborated on here.

The Fish

Taxonomy

Fish systematics is at the same stage as that of North American fish fauna a century ago (Böhlke et al. 1978). Even larger commercial species have been confused with synonyms or inadequately described species, and many common names in Table 1 have been more consistent in the appropriate locality than the scientific ones.

Roberts (1972) estimated there were approximately 1300 species recorded in the zoological records from the Amazon basin. Böhlke et al. (1978) considered that at least 30 % of the species are still undescribed.

In the Amazon basin about 85 % of the fish species belong to the superorder Ostariophysi, of which 43 % are Characoidei, 39 % Siluriformes and 3 % Gymnotoidei. The remaining 15 % are distributed among the families Lepidosirenidae, Osteoglossidae, Nandidae, Cichlidae, Cyprinodontidae, and Poeciliidae (Roberts 1972), plus Sciaenidae, Engraulidae, Clupeidae, Soleidae, Synbranchidae, Tetraodontidae, Gobiidae, and Potamotrygonidae. Lowe-McConnel and Howes (1981) and Barthem (1985) contain recent species lists.

Life Histories

Since the mid 1970's biological studies have accelerated. However, the majority are at present difficult to relate quantitatively to the species impact on food resources, energy transfer, and interactions. Junk (1984a) gives a brief review of recent literature. Bayley (1989) provides a brief description of aquatic environments in the basin.

Salient features of life histories of the larger fish species do not deviate much from the general descriptions of other tropical river–floodplains (Welcomme 1979), except for two factors. Although all tropical and temperate river–floodplains contain abundant detritivorous fish species, none appear to be so specialized or abundant as the Prochilodontidae and Curimatidae of S. American systems (Azevedo et al. 1938; Lowe-McConnell 1975; Goulding

TABLE 1. Common commercial fish species and species groups.

Family, Sub-order or Order	Common Name[a]	Species or Genus
Serrasalmidae, Characoidei		
	tambaquí	*Colossoma macropomum*
	pirapitinga	*Piaractus brachypomus*
	pacú	*Mylossoma, Metynnis, Myleus*
	piranha	*Serrasalmus, Pygocentrus*
Prochilodontidae, Characoidei		
	jaraquí	*Semaprochilodus taeniatus, S. insignis*
	curimatã	*Prochilodus nigricans*
Curimatidae, Characoidei		
	branquinha	*Potamorphina, Curimata*
Hemiodontidae, Characoidei		
	cubiu	*Anodus melanopogon*
	urana	*Hemiodus, Anodus*
Anostomidae, Characoidei		
	aracú	*Schizodon fasciatum, Leporinus, Rhytiodus*
Characidae, Characoidei		
	matrinchã	*Brycon* cf. *melanopterus*
	jatuarana	*Brycon* sp.
	sardinha	*Triportheus*
Erythrinidae, Characoidei		
	traira	*Hoplias malabaricus*
Pimelodidae, Siluriformes		
	piraiba	*Brachyplatystoma filamentosum*
	piramutaba	*Brachyplatystoma vaillantii*
	dourada	*Brachyplatystoma flavicans*
	filhote	*Brachyplatystoma* sp.
	surubim	*Pseudoplatystoma fasciatum*
	capararí	*Pseudoplatystoma tigrinum*
	pirarara	*Phractocephalus hemioliopterus*
Doradidae, Siluriformes		
	bacú	*Megalodoras, Pterodoras, Lithodoras*
	cuiú-cuiú	*Oxydoras niger*
Hypophthalmidae, Siluriformes		
	mapará	*Hypophthalmus*
Loricariidae, Siluriformes		
	acarí, bodó	*Pterygoplichthys, Plecostomus*
Sciaenidae, Perciformes		
	pescada	*Plagioscion* spp.
Cichlidae, Perciformes		
	tucunaré	*Cichla ocellaris, C. temensis*
	acara-acú	*Astronotus ocellatus*
	acará	*Cichlasoma, Chaetobranchus, Uaru, Geophaqus*
Clupeidae, Clupeiformes		
	apapá	*Pellona* spp.
Arapaimidae, Osteoglossiformes		
	pirarucú	*Arapaima gigas*
Osteoglossidae, Osteoglossiformes		
	aruanã	*Osteoglossum bicirrhosum*

[a] Common names used in Manaus area; many of these are expanded to describe different species within a group.

1981; Ribeiro 1983). Common species of these families begin feeding on fine detritus when only 2–3 cm long (Bayley 1983) and continue with this specialized diet into adulthood when individuals attain 1–4 kg. Araujo-Lima and Hardy (1985) deduced that *Semaprochilodus insignis* 1.5–5 cm long depend on detritus in addition to other food items. Second, other systems do not contain the variety or quantity of species adapted to consuming tree fruits in Amazon floodplains (Goulding 1980; 1983).

The most productive aquatic environment is the várzea (Fittkau et al. 1975; Bayley 1989), which is the floodplain influenced by the turbid "white water" rivers, which includes the Amazon. Important features which the várzea has in common with other tropical floodplain fish communities (Lowe-McConnell 1975; Welcomme 1979) are the large quantity of piscivores (Barthem 1981; Goulding 1981; Bayley 1983), the limited number of specialized planktivores or herbivores (Bayley 1981a), and the abundance of many species tolerant of low oxygen conditions (Kramer et al. 1978; Braum and Junk 1982; Werder and Saint-Paul 1979).

Piscivorous fish, most of which also consume *Macrobrachium* prawns (Worthmann 1982; Bayley 1983) constitute 35 % of the biomass averaged throughout the year in the várzea (Bayley 1983) and 35 % of gillnet fleet catches in a variety of várzea and "ria lake" habitats (Barthem 1981). The various commercial fisheries are poor indicators of the abundance of these "piscivores", which constitute 100 % of the large catfish fisheries in the upper Amazon basin in Brazil (Bayley 1981a) and the upper R. Madeira (Goulding 1981) but only 4 % of the yield consumed in Manaus (Petrere 1982) and 12 % in Itacoatiara (Smith 1981).

A preliminary analysis (Bayley 1983) indicated that at least 75 % of the production of fish and decapods up to 24 cm long in the várzea was consumed for by "piscivores", even though the latter did not include non-piscine consumers or omnivorous fish such as piranhas which include some fish in their diet (Goulding 1980). Junk et al. (1983) have suggested that low oxygen tolerant species use such environments as refuges from predation. Some piscivorous fish do avoid low oxygen conditions, but many other piscivores, especially birds, are attracted in large numbers to areas where fish are swimming slowly at the surface due to low oxygen conditions (pers. obs.).

Fish migrations in the Amazon involve many commercial species. Mark and recapture experiments are expensive due to the high mortality rates in tropical floodplains (e.g. Lagler et al. 1971) and the cost of the education and rewards necessary to obtain returns in such a vast region. Carvalho (1983) reported only 6 recaptures of 1 123 marked fish despite regional publicity, and all recaptures were of the sedentary *Potamorhina pristigaster*.

Various theories have been forwarded (Goulding 1980; Ribeiro 1983) based on direct observations and fishermen's reports of some parts of the life cycles of large characoids. Petrere (1985a) reviews migration studies in the Neotropics, noting the complexity of migration patterns and their dependence on the environment as well as on the species concerned.

Two broad categories of life histories are apparent (Goulding 1980; 1981; Bayley 1983; Ribeiro 1983; A. Guedes dos Santos, pers. comm.). Most larger Ostariophysi species are total spawners which reproduce in the main channel or the várzea prior to or during the rising water phase. Different species have preferred spawning periods within this period (Bayley 1983). The rising floodwaters aid in spreading the progeny over the várzea habitats, in particular in littoral habitats which continually cover new ground. Growth rates are highest during this period, and are positively related to the rate of rise of water level (Bayley 1983). Adults and subadults build up fat reserves during the rising water period, some species feeding in black and clear water habitats. The drawdown period results in movements of adults and juveniles to the main rivers, floodplain lakes, and permanent tributaries. Subsequently some species undergo longitudinal migrations in major channels, and some enter black or clear water tributaries.

Except for piscivorous catfish, the large rivers are mainly used as "highways", low water refuges (in addition to residual lakes and streams for some species) and points of departure for progeny in the case of white water rivers. Feeding opportunities are limited for non-piscivores, even near the shoreline, compared with várzea and igapó ("black water" forest) habitats.

The second category consists of more sedentary species, and include Cichlidae, smaller Ostariophysi, Osteoglossidae and other small taxa. They include partial spawners with varying degrees of parental care. They tend to have a less well-defined spawning season. They are not commonly observed in white water rivers. Their movements are confined to floodplain habitats, in particular várzea lakes, ria-lakes, flooded forest and adjacent streams and channels.

These two categories do not correspond to the "white" and "black" fish groups described from S.E. Asia by Welcomme (1985) because both categories contain species which can withstand partially or completely deoxygenated conditions. The first category corresponds to the "white" group in other respects, but many species of this category undergo aquatic surface respiration to survive when dissolved oxygen is depleted (Kramer et al. 1978; Braum and Junk 1982; Junk et al. 1983).

Delimitation of populations or stocks is allied to the problem of migration studies. Very little information is available at present, but there is strong meristic inference of different stocks of one of the most migratory species, *Semaprochilodus insignis*, whose samples were only 40 km apart (Bayley 1983). Indications of population differences have also been noted for *Plagioscion squamossisimus* and *P. montei* by Worthmann (1982) and for *Hemiodus microlepis* by Johns (1982).

The Fisheries

There are numerous, diverse food fisheries in the basin which can be defined by economical and geographical criteria. Commercial and small market/subsistence fisheries are dominated by Brazil and Peru, which in 1980 had 6.0×10^6 and 1.2×10^6 basin inhabitants, respectively. The most important are the diffuse, artisanal fisheries which provide fish for subsistence and small, local markets. Most of the rural and small town human population lives on the non-flooded, "terra firme" land bordering the várzea or the major rivers, and many are part-time fishermen. Their yields do not feature in government statistics, but data are now available for their estimation. In addition there are a variety of more commercialized fisheries which concentrate on certain species, but most of them still depend on artisanal fishing techniques. Some of these fisheries are reported in government statistics.

Local Market/Subsistence Fisheries

Fish are the main source of animal protein for the human population in most parts of the basin. Numerous surveys of per capita consumption have been made (Table 2) which are surprisingly consistent within strata considering the different sources of information. Any fish products from other sources, such as salted cod or canned sardines, were recorded separately, so these could be excluded for this analysis. Peripheral areas within the basin, such as the "selva alta" of Peru and Rondônia in Brazil, have lower consumption rates (Table 2) due to greater distance from floodplains or traditions of certain immigrants (Goulding 1979), but they are still higher than world averages (Robinson 1984). In the lowlands, consumption tends to be higher in rural areas bordering or within floodplains, and lower in riverine cities, in particular for higher socio-economic groups.

Per capita consumption data based on interviews in homes is a useful but usually ignored tool for estimating yields of diffuse fisheries where the "traditional" approach (e.g. Bazigos 1974; Chapman 1981) based on catch per effort and gear surveys is prohibitively expensive. Sampling error in the latter approach is high (Table 3) because there are large variances for both daily catch per effort, and the total effort estimates which often require data from expensive aerial counts, which in turn need to be corrected using additional ground counts to allow for boats hidden under trees (Kapetsky 1981). The coefficients of variation from catch per effort data in Table 3 do not account for additional variance in the proportion of canoes which were fishing at the time; this is difficult to estimate without bias.

Most consumption estimates are reported as means, but random samples of household interviews from waterside communities in the Neotropics (Table 3) indicate a much lower sampling error than the traditional approach. The total error is much smaller for two reasons. The consumption estimates are multiplied by the human population, whose error is negligible in comparison. Conversely, catch per effort is multiplied by total effort estimates which are themselves subject to large error in dispersed fisheries. Second, families interviewed are asked their average fish consumption during a given time period, whereas individual catch per effort varies widely from day to day and between individuals. The cost of sampling a given number of homes is similar to that of sampling the same number of landings, but the latter are typically less convenient because fish are only landed during restricted times of the day, and when the fishermen are least disposed to giving interviews.

Although the variance of estimates from the socio-economic approach compares favorably, possible biases need to be checked. Discards are virtually nonexistent in

TABLE 2. Per capita fish consumption estimates.[a]

Fresh round Wt. per capita per day (g)	Region	Source
	Lowland regions (Amazonas, Pará States, Brazil; "selva baja" (<350 a.m.s.l.), Peru)	
167	Manaus city, Brazil (low income group)	Shrimpton et al. (1979)
155	Manaus city, Brazil (middle income group)	Shrimpton et al. (1979)
117	Manaus city, Brazil (high income group)	Shrimpton et al. (1979)
194	Itacoatiara and rural area within 60 km	Smith (1979)
99	Iquitos and Pucallpa cities, Peru	Hanek (1982)[b]
73	"selva baja" non-riverine, Peru	Hanek (1982)[b]
78	Iquitos, Peru	Eckmann (1985)[c]
89	Pucallpa, Peru	Eckmann (1985)[c]
74	Lowland, towns, Peru	Eckmann (1985)[c]
185	Lowland, rural, Peru	Eckmann (1985)[d]
277	"Selva baja" (lowland) riverine, Peru	Hanek (1982)[b]
175	R. Pichis, "selva alta"/"baja", Peru	Gaviria (1980)
122	R. Palcazu, "selva alta"/"baja", Peru	IMARPE (1972)
	Upland regions, and others distant from floodplains (Rondônia, Roraima States, Brazil; "selva alta", Peru; Bolivia. These regions import a significant quantity of fish from floodplain areas downstream, or in the case of Bolivia have competitive beef prices.)	
24	Porto Velho city, Brazil	Goulding (1979)
18	"selva alta" urban, Peru	Hanek (1982)[b]
31	Tarapoto town, "selva alta", Peru	Bayley (1984)
39	"selva alta" rural, Peru	Hanek (1982)[b]
11	Trinidad, Bolivia[e]	

[a] Where corrections were not made, 10% dressing allowance was made for fresh fish and any dried fish component was corrected to whole fresh weight using a conversion factor of 2.5.

[b] Using direct estimates of total fish consumed in different areas of Peru (Escobar 1965; Beuzeville 1973; Bergman 1978; Chirif 1979 *in* Hanek 1982) or fish purchases in cities from a national survey ENCA (1972).

[c] Using data on fish purchases by consumers.

[d] Using 3, plus estimates based on protein "requirement" estimated by the Peruvian Ministry of Health combined with an estimate that four times the fish purchased are caught and consumed directly.

[e] From M. J. Harvey (pers. comm.), Fisheries Adviser, based on complete market statistics in 1985.

TABLE 3. Sampling errors of canoe landings and house surveys of per capita consumption.

Method	Sample size	CV	Samples needed for 95% confidence range within ±10% of the mean	Source
Canoe landings from large rivers, Peruvian Amazon	30	187%	1 340	Bayley (1981c)[a]
Canoe landings from intermediate rivers, Peruvian Amazon	30	268%	2 760	Bayley (1981c)[a]
House survey in R. Palcazu Indian community, Peruvian Amazon	8	33%	42	IMARPE (1972)[b]
House survey in a riverine communities on R. Paraguay	20	60%	140	Bayley (1985)[c]
House survey in two lakeside communities L. Gatún, Panamá	22	99%	380	Bayley (1986)[c]
House survey in two lakeside community, L. Madden, Panamá	11	50%	96	Bayley (1986)[c]

[a] Statistical unit of catch per day based on the product of catch per unit effort, number of canoes, and proportion of time canoes were fishing; variance of and correlation between the first two components only were available; data supplied by FAO project PER/76/022 used in Chapman's (1981) catch assessment survey.

[b] The 8 samples were taken during different weeks in the year; these were the mean of 5 families surveyed each time.

[c] Randomly selected householders were asked to estimate the whole weight of fish typically consumed (purchased and/or captured from the river or lake concerned) and the number and age distribution of occupants; the statistical unit of whole fresh weight/average person/day calculated as in Bayley (1986).

local market/subsistence fisheries due to their proximity to the market or village. Even in commercial fisheries, economic factors have contributed to a reduction in discards such as in Manaus (Bayley 1981a). Table 4 compares various yields which have been independently estimated using landings which supply the same human population. Eckmann's (1985) estimate is more deviant, which could be partly explained by a calculation error in his Table 6 and the fact that his human consumption estimates were largely made indirectly. Otherwise, the comparisons indicate good concordance, especially considering that the per capita estimates were made several years previous to those of the landings.

Combined local fisheries account for 61 % of the total yield (Table 5). Yet this proportion was based on data (Table 2) which, with the sole exception of the data from IMARPE (1972), were neither collected by a fisheries agency nor collected for fisheries purposes. To obtain this information by interviewing fishermen at the multitude of separate landing points and making total boat counts with any useful level of accuracy is beyond the resources of the countries concerned. Conversely, well-designed household surveys can estimate yields from dispersed fisheries as well as additional information such as effort by gear and man-hours, species composition, and proportion of consumption caught or purchased.

Large Commercial Fisheries

These fisheries are characterized by centralized landing areas at major cities or fish exported from the basin at particular localities, and comprise 39 % of the total amazon yield (Table 5). The higher cost of fishing and the more selective markets result in a smaller number of species dominating their yields. However, with the exception of the Pará fishery, the fisheries are supported by a variety of gear, including artisanal techniques, based on canoes with larger boats (mother ships) being used only to house fishermen and transport the catch (Petrere 1978a; Hanek 1982; Eckmann 1985).

TABLE 4. Comparison of yields (t) based on per capita consumption and independent estimates based on catch samples.

Locality	Yield from per capita consumption	Yield from landing statistics
Manaus City, 1976	25 600[a]	30 200[b]
Manaus City, 1977	27 700[a]	21 700[b]
Manaus City, 1978	29 900[a]	22 400[b]
Peruvian Amazon, 1980[c]	59 000[d]	52 700[e]
Peruvian Amazon, 1980[c]	34 200[f]	52 700[e]

[a] Per capita estimates from Shrimpton et. al. (1979) (Table 2); human population estimates interpolated from national censuses in 1970 and 1980 (IBGE 1981).

[b] Manaus port landings (Petrere 1982); minor additional landings, prevalent in 1977 and 1978, could not be recorded.

[c] Estimates from Loreto and Ucayali departments, comprising 94 % of the Peruvian Amazon floodplain area (Bayley 1981b).

[d] Stratified per capita estimates, including those based on "selva alta" consumption from Hanek (1982) (Table 2); human population estimates interpolated from national censuses in 1972 and 1981 (INE 1982).

[e] Based on Guerra et al. (1981) from Catch Assessment Survey in an area comprising 26 % of the total floodplain area (Bayley 1981b), scaled up to total floodplain area of Loreto and Ucayali departments. Chapman (1981) extrapolated Catch Assessment Survey data on the basis of sizes of small, medium, and large rivers and floodplain lakes to produce an estimate of 342 000 t, excluding the commercial fleet yield.

[f] Eckmann (1985): per capita consumption was estimated separately from fish purchases and fish caught (Table 2); human population was extrapolated from 1972 data; his Loreto department includes Ucayali department.

The species compositions of these fisheries cannot be regarded as representative of the larger local market/subsistence fisheries. They are even very distinct among themselves (e.g. Goulding 1981: Table 4.1). Even the most diversified commercial fishery serving Manaus has a different catch composition from that using artisanal gear only (Table 6), even though in the latter case the more valuable species which are sold in the large city markets of Itacoatiara are included. In more remote areas valuable species such as *Colossoma* are frequently sold to commercial fishing units which sell them in cities such as Manaus, while cheaper species are consumed locally.

The reliability of commercial fisheries data is variable. The data discussed below are from those years when government statistics have been checked and corrected for discrepancies (e.g. Petrere 1978a; 1985b).

Manaus Fishery

This is the largest commercial fishery and has been the most accurately monitored during 1976–78. A longer data series exists (SUDEPE 1985), which suggests no trend in total yield from 1975–80, but fishermen's estimates are not corrected and there are no appropriate effort data such as fishermen-days (Petrere (1982).

The Manaus yield was 13 % of the total amazon yield, and 27 % of the total yield within its range of activity in Amazonas State (Table 5). For a centralized, commercial fishery, the number of species and diversity is notable (Tables 1,6) due to the different fishing methods which have been adapted to the enormous variety of habitats in the floodplains and rivers. However, the diversity would be much higher but for market preferences and preservation limitations for some species.

Larger boats cover impressive distances for a few valuable species. In the mid 1970's, the maximum distance reached was approximately 1 700 km by river from Manaus (Petrere 1978a); presently it is about 2 500 km (A. Jacauna, pers. comm.). These trips concentrate on the valuable tambaquí, *Colossoma macropomum*, individuals of which attain 30 kg. The large distances travelled is not a recent phenomenon. Fishing in remote areas has traditionally occurred at a much lower intensity (Goulding 1983).

There are various, more intense fisheries closer to Manaus. In floodplain lakes effort has been directed towards the pescada, *Plagioscion* spp., tucunaré, *Cichla* spp., and other large Cichlidae species (Petrere 1978a, 1978b). In rivers and connecting channels, seines account for jaraquí, *Semaprochilodus* spp., and seines or gillnets catch curimatã, *Prochilodus nigricans*, and various species of Curimatidae, Anostomidae and Hemiodontidae.

In 1978, 87.9 % of the trips in a total of 5 205 occurred inside a radius of 500 km from Manaus (as distance travelled) and accounted for 60.8 % of the total Manaus

TABLE 5. Fish yields (t) and floodplain areas by river basin and country in 1980[b].

Source of captures	Flooded area (km^2)[a]	Local market, subsisttence yield[b]	Yield to Manaus[c]	Other commercial yields[d]	Total yield	Yield/area kg•ha^{-1}
R. Solimões, Japurá Jutai, Içá — Brazil	49 530	17 360	12 410	10 380	40 350	8.1
R. Juruá — Brazil	6 710	4 670	1 560	1 840	8 070	12.0
R. Purus—Brazil	9 460	4 720	5 030	2 760	12 510	13.2
R. Amazonas, Amazonas State — Brazil	15 350	16 050	3 920	2 590	22 560	14.7
R. Madeira — Brazil	2 230	1 960	1 250	940	4 150	18.6
R. Negro — Brazil	(7 030)	2 310	590	—	2 900	4.1
R. Branco — Brazil	(1 130)	690	15	—	715	6.3
R. Amazonas, Pará State — Brazil[e]	21 720	29 060	—	16 600	45 660	21.0
Amazon basin — Peru[f]	38 800	44 400	—	14 600	59 000	15.2
R. Putumayo — Colombia and R. Javarí — Brazil[g]	2 800	—	—	—	—	—
Amazon basin in Bolivia[h]	33 760	2 070	—	620	2 690	0.8
"white water" — influenced floodplain area =	180 360 (2.6% of basin area)			Total yield =	198 650	

[a] Estimates derived from Bayley and Moreira (1980), Bayley (1983) and Petrere (1982) for Brazil and Bayley (1981b) for Peru and this paper using LANDSAT, side-scanning radar (RADAMBRASIL) images and ground truth observations; they include channels but exclude poorly drained peripheral areas, in particular swamps associated with the palm tree *Mauritia flexuosa*, which are inhospitable to most of the fish biomass (Bayley 1981b); R. Negro and R. Branco estimates not counted in total because their floodplains are not of the highly productive, várzea type.

[b] Brazil estimates based on a per capita consumption of 170 g • person^{-1}•d^{-1} (average of Manaus low and middle income and Itacoatiara estimates in Table 2), except for the non-traditional communities dominating the R. Madeira and R. Branco where the Porto Velho estimate of 24 g•person^{-1}•d^{-1} (Table 2) was used. Human population statistics for 1980 from IBGE (1981); in Peru, Hanek's (1982) stratified estimates (Table 2), including "exports" to the "selva alta", were applied to human population estimates for 1980 interpolated from 1972 and 1981 national census date INE (1982).

[c] Based on mean of corrected Manaus Port data (Petrere 1982) for 1976–78, including small amounts caught in tributaries; the longer time series from SUDEPE, Manaus (in Junk 1984a) is uncorrected, containing errors up to 20%, but suggests no trend in total Manaus yield between 1975 and 1980.

[d] Amazonas State yields dominated by large catfish (*Brachyplatystoma* and *Pseudoplatystoma* spp.) exports to Colombia and S. Brazil, and *Arapaima* exports to northeast Brazil (Bayley 1981a); in Pará State, commercial fishery dominated by *Brachyplatystoma vaillanti* fishery SUDEPE (1985) (1980) yield given, mean for 1976–84 = 19 700 t); in Peru, most commercial catch consumed in Iquitos and Pucallpa (Hanek 1982).

[e] Conservative estimates of local yield based on 1980 population bordering the R. Amazonas in Pará down to the beginning of the delta near Carrazedo using consumption rate of 170 g•person^{-1}•d^{-1}; flooded area based on the same, ignoring clear and black water tributaries and mouth lakes not influenced by white water.

[f] Major part of flooded area from catchment draining into upper Amazon river (33 250 km^2), the remainder from Peruvian parts of R. Putumayo, R. Yavarí and R. Madre de Dios (Bayley 1981b) where fishing intensity is extremely low.

[g] Reports indicate that fishing is negligible in these remote areas.

[h] Bolivian estimates based on 1984-85 data from M. J. Harvey, Fisheries Adviser (pers. comm.); floodplain areas relatively large due to very flat topography; total area based on R. Mamoré estimate of 8 760 km^2; subsistence/local market estimate based on Trinidad per capita estimate in Table 2; most of the commercial catch is shipped to La Paz or exported to Brazil.

catch. Inside this radius, *Colossoma* accounted for 23.8 % of the total catch, which was exceeded by *Semaprochilodus* spp. with 34.7 %. Outside this radius, *Colossoma* accounted for 56.5 % of the total catch and *Semaprochilodus* 17.7 %. Inside the radius, the catch rate was 3.2 t per trip and outside it was 9.3 t per trip (Petrere 1982). However, the nearer trips take 1–3 days compared with the distant ones which may take 1–3 months and cost more in fuel and travel time. Also, some species in the proximate fishery, notably *Cichla* and *Plagioscion* command even higher prices than *Colossoma*. They are not fished farther afield due to difficulty in quality control.

Petrere (1978a) found that the lampara seine — employed in lakes and rivers, often in the mouths of tributaries during the spawning season — accounted for 48.6 % of the total catch and accounts for most of the Characoidei species. Large mesh gillnets, which are mostly employed in the fishery of *Colossoma* in várzea lakes and openings in the flooded forest, accounted for 34 % of the catch. The harpoon, jig, rod and line, and cast net also feature in lake fishing, and account for a variety of species.

The beach seine is mainly employed during seasonal migrations of *Semaprochilodus*, *Colossoma*, and *Brycon* spp. Where beaches are not available, fishermen often clear good fishing spots of trees and brush at low water, so that nets can be used at high water to catch passing migratory

TABLE 6. Comparison of species composition by weight between a commercial fishery and one using artesanal gear only.

Taxa	Manaus commercial yield (%)[a]	Artesanal fishery yield (%)[b]
Colossoma macropomum	41.1	7.3
Semaprochilodus spp.	23.9	0.0
Prochilodus nigricans	9.4	20.3
Mylossoma, Metynnis, Myloplus	4.9	2.3
Piaractus brachypomus	4.7	1.7
Cichla spp.	3.3	7.2
Brycon spp.	2.6	0.1
Anostomidae spp.	2.1	0.8
Triportheus spp.	2.0	0.1
Osteoglossum bicirrhosum	1.5	21.7
Curimatidae spp.	1.3	0.2
Plagioscion spp.	1.0	1.4
Cichlidae spp. (exc. *Cichla*)	0.6	6.2
Arapaima gigas	0.4	6.1
Loricariidae spp.	0.4	14.4
Hemiodontidae spp.	0.3	0.0
Hypophthalmus spp.	0.2	0.5
Oxydoras niger	0.1	1.7
'Piranha' spp.	0.01	1.8
Other spp.	0.2	6.2

[a] Mean of 1976–78 yields to Manaus (Petrere 1982), based principally on lampara seines, large mesh gillnets and large beach seines.

[b] Smith (1981: Appendix 4); he recorded catches while accompanying fishermen in 58 canoe excursions in 1977; data for typical artesanal gear: gill net, castnet, gig, harpoon, bow and arrow, suspended trotline, handline and pole are included; lampara seine, beach seine and bottom trotline are excluded because they are not typical of gear used for local market/subsistence fisheries but are used to supply commercial fish for large cities or exports.

TABLE 7. Estimated total commercial landings (t) and total effort for *Brachyplatystoma vaillantii* by the Belém commercial fleet from 1972–84 (from SUDEPE 1985).

Year	Total landings (t)	Effort in days
1972	8 351	1 424
1973	13 331	2 191
1974	17 157	4 046
1975	19 417	4 344
1976	22 052	4 300
1977	28 829	4 308
1978	22 608	4 100
1979	20 835	4 613
1980	16 608	6 010
1981	16 228	3 639
1982	17 658	3 250
1983	19 215	3 914
1984	13 479	4 106

fish. This method partially compensates for the lower market supply during rising water levels, and distinguishes this fishery from others in the middle and upper basin. The beach seine — measuring up to 500 m long by 13 m deep — was responsible for 9.3 % of the total catch in 1976.

Owing to the increased fish dispersion during high water, there is a negative correlation between the quantity of fish caught and the water level, particularly during the rising water period. This correlation is highly significant for some species when analyzed separately from total catch (Petrere 1982). The maximum distances travelled by the Manaus fishing fleet tend to occur during the high-water season, whereas the fishermen are more concentrated during the low-water season when fishing is more economical nearer to Manaus (Petrere 1982).

Vegetation and lake morphology play major roles in fishing strategy, in particular for large *Colossoma* spp. and Serrasalmidae spp. (including piranhas) which eat a variety of fruits. In the case of "black water" terra firme lakes, which would be considered by limnologists to be a "poor" environment, fishing is successful under the flooded forest in the high-water season (Goulding 1980). Adults and subadults of the abundant *Semaprochilodous* spp. feed in the littoral zones of black waters (Ribeiro 1983) and support an important fishery in the lower R. Negro.

Floodplain area explained 66 % of the variance of catch by river (Petrere 1983a). After accounting for floodplain area, the total catch per river was also strongly correlated ($P<.01$) to annual number of trips per river, the annual number of fishermen who operated in each trip per river, and the length of each river covered in each year by the Manaus fishing fleet.

The only Central Amazonian fish for which there is a yield-per-recruit study is *Colossoma macropomum* (Petrere 1983b). Using length-frequency data, the only kind of information available, it was concluded that there was no growth overfishing. The average individual weight landed at the market in Manaus was 8.4 kg in 1978. Currently it is estimated to be 6 kg (F. P. Castelo, pers. comm.). *C. macropomum* is still the most important fish species landed at the Manaus market.

Commercial Fishery in Peru

This fishery was first described by Hanek (1982). Eckmann (1985) provided some additional comments and time series. The commercial fishery accounted for 25 % of the total yield in the Peruvian Amazon (Table 5). From data in Hanek (1982) it is estimated that 476 fishing economic units consisted of 828 motorized boats and 694 canoes and supported about 2 600 fishermen who worked full time at least during low water. This compares with 49 924 fishing economic units in the local market/subsistence fishery, using 51 200 canoes or boats and involving about 78 700 part-time fishermen.

Characoids dominated the catch in Iquitos as in Manaus, and comprised 75 % of the catch in 1980. Although total yield at Iquitos has remained between 2 000 and 3 000 tons from 1974–80, Eckmann (1985) notes that the detritivores, *Prochilodus nigricans* and Curimatidae spp., increased mainly at the expense of *Colossoma* and *Brycon* and attained 67 % of the yield by 1980.

The main fishing gears employed are the cast-net, gillnet, bow and arrow, haul seines, and "deepwater drifting gillnets". The latter technique, introduced from Brazil, involves drifting a large mesh net down snag-free sections of the main river channel to catch large catfish. Seasonal variation in catches is high (Eckmann 1985) and is greater than in the Manaus fishery because of fewer high water techniques being used.

Fisheries in the Mouth of the Amazon

A 16-year time series has been recorded for the largely industrial fishery which targets the piramutaba, *Brachyplatystoma vaillantii*, in the delta/estuary region (Table 7). Other, more recent industrial fisheries based in Belém and Amapá Territory concentrate on the dourada (*B. flavicans*) farther offshore and seasonally in the river, but data are not being collected (Goulding, pers. comm.).

Most of the *B. vaillantii* commercial yield is provided by pair trawls at 7–12 m depth are operated from boats averaging 108 gross tonnage (Castillo 1978). Fishing extends to Cabo Norte which is close to the marine coast. Although it is small compared with the local market/subsistence fishery in Pará upstream of the delta (Table 5), it is important for foreign exchange since most of the yield is exported to the United States and Europe. Small quantities of dourada (*B. flavicans*), gurijuba (*Arius parkeri*), bagres (Ariidae spp.), and pescada (*Plagioscion* spp., *Cynoscion* spp.) are also caught.

This most industrialized fishery in the basin also discards more fish than any other. Fish smaller than 40 cm long are rejected since they are not suitable for filleting. The discard rate has reached 56 % (Castillo 1978).

The artisanal fishery, which accounted for 14 % of the 1984 commercial yield of *B. vaillantii* (Table 7), has vessels that vary from canoes to small vessels of about 20 t. They are more restricted to the coast and employ bottom-set, drifting gillnets, and occasional longlines. The catch is more diverse but is still dominated by *B. vaillantii*. In the high-water season (January–May) effort is concentrated mostly on the larger Pimelodidae and *Plagioscion*. At low-water (July–November) more marine fish are caught (Ariidae, *Cynoscion* spp., Carangidae, Carcharhinidae, Pristidae, Mugilidae) due to greater incursion by the sea. Some fishermen go up the Amazon following high-water migrations of *B. vaillantii* and *B. flavicans*.

The data of total landings and total effort (Table 7) were adjusted to the Schaeffer model employing the "GM" regression (Ricker 1973). The maximum sustainable yield of 19 400 $t \cdot yr^{-1}$ corresponded to 4 567 days of effort. If the relationship between adult and juvenile piramutaba does not change, this estimate indicates that the present level of effort would not result in growth overfishing with the present cod end mesh size of 99 mm.

The artisanal fishery supplying small markets and subsistence around Belém is dominated by *Lithodoras dorsalis* which are mainly caught in weirs with the assistance of the tidal cycle (M. Goulding, pers. comm.). Estimates are not available for any subsistence fisheries in this region, which include an unknown proportion of marine species.

Other Commercial Fisheries

These fisheries comprise various piscivorous species. An extensive "deepwater drifting gillnet" fishery for large catfish in the large "white water" rivers of Amazonas State supplies markets in Bogotá, Colombia and southern Brazil and amounted to 9 000 t in 1977 (Bayley 1981a). The catch is dominated by *Brachyplatystoma filamentosum*, with smaller quantites of *B. flavicans, Phractocephalus hemioliopterus* and *Pseudoplatystoma* spp. Catfish are generally rejected by most Brazilian residents in the basin (Smith 1981). These fish are top piscivores, and it is uncertain how long this fishery will be maintained.

The traditional fishery for the large piscivore *Arapaima gigas*, using harpoon and occasionally gillnets, mainly supplies northeast Brazil. Its yield estimate of 6 000 t (Bayley 1981a) is approximate because closed season and size limit regulations result in a minority of exports from the region being officially recorded.

Goulding (1979, 1981) describes the fisheries for *Brachyplatystoma flavicans* in the Teotônio rapids and for various of characoids in the flooded forest in the upper R. Madeira which supply Pôrto Velho.

Physical Characteristics and Potential Yields

Potential yield cannot be reliably predicted on the basis of our present knowledge of trophodynamics or traditional fish population dynamic models, since the system is complicated by the variety of life histories, interactions, and vulnerabilities among species in addition to the diversity of fisheries, gear types, and our inability to distinguish stocks.

Using appropriate scaling, comparative methods show the most promise. Floodplain area, basin area or main channel length are significantly correlated with total yields of African river floodplains (Welcomme 1975; 1976; 1979), despite differences in exploitation. Biological reasons for comparing African with S. American systems were discussed in Bayley (1981a). Measuring basin area or main channel length is straightforward using maps of appropriate scale.

Floodplain Areas

Areas of várzea floodplains (Table 5) were discernible from either LANDSAT or side-scanning radar images which indicate topography and geomorphological features (Bayley and Moreira 1980; Bayley 1981b; Petrere 1982; Klammer 1984). Petrere (1982; 1985b) used an interpretation of flooding by RADAMBRASIL (1976) from side-scanning radar for rivers in Amazonas State. This was checked independently (by PBB) using near infra-red, 1:500 000 images of LANDSAT for the R. Amazonas in Amazonas State using methods described in Bayley (1981b). The area — which included the várzea, parts of ria-lakes (Klammer 1984) influenced by white water, and the main channel, but not black water tributaries or marginal swamps — was only 10 % less than Petrere's (1982) estimate. His estimates for other Amazonas State rivers are corrected by a similar amount in Table 5.

The estimates in Table 5 are conservative in that they account only for the more productive várzea areas which are influenced by "white waters"; the R. Negro and R. Branco are not included in the total. Peripheral swamps, which are very significant in Peru (Bayley 1981b), are very acidic, have low or zero oxygen, and poor nutrient supply (Junk 1983), are excluded since they can account for only a negligible part of the fish biomass and productivity of its food. Kramer et al. (1978) noted the limited fish fauna which are purely air-breathing. This is probably due to the widespread association of hydrogen sulphide with deoxygenated waters (Fittkau et al. 1975). In addition, estimates in Table 5 exclude "black", "clear", and small "white" water rivers. The amazon delta itself was excluded because its morphology and hydrology are very distinct (Sioli 1966), making it difficult to estimate without more ground truth data.

Potential Yields

Welcomme (1976) defined three "extensive" African floodplain systems as flooding 1.8–2.4 % of the basin area. The same systems, the Niger, Senegal, and Ouémé, were redefined as flooding 2.5–3.8 % of the basin area (Welcomme 1979), but by either definition the conservative Amazon basin estimate of 2.6 % (Table 5) qualifies. These "extensive" systems produce about three times the yield of "normal" systems when scaled by basin area (Welcomme 1976). Regression of the log-transformed values of yield on basin area and main channel length (Welcomme 1976: Appendix 1) from these three systems produces the following relationship in original units:

Yield (t) = .826(basin area,km^2)$^{.846}$(r=.9870 $s_{x \bullet y}$=.328)
Yield (t) = .183(main channel length,km)$^{1.617}$(r=.9997 $s_{x \bullet y}$=.051)

The $s_{x \bullet y}$ values in transformed units are similar to, or less than Welcomme's (1976) estimates for the larger data set of "normal" floodplains. First order approximations of amazon basin yields based on these relations are 514 000 and 269 000 t•yr,$^{-1}$ respectively, using scaling parameters in Sioli (1984). This would suggest that the Amazon river length is short for the basin size, and indeed much of the main channel in Brazil does not meander (Sioli 1984). Mean theoretical yields per floodplain area (Table 5) are 28 and 15 kg•ha,$^{-1}$ respectively.

In the Peruvian part of the basin draining into the R. Solimões, 3.9 % of the basin area is flooded (Bayley 1981b). Predicted yields based on the above relations, using parameters in Bayley (1981b), are 86 000 and 74 000 t•yr^{-1}, which correspond to 26 and 22 kg per flooded area, respectively. Both these estimates and those for the whole basin are lower than Welcomme's (1979) norm of 40–60 kg•ha^{-1}. This is due to more extensive flooding in Peru, and the fact that the estimates of flooding are conservative since they are restricted to areas influenced by white water. Total flooding in the Peruvian basin draining into the upper R. Amazon is 12 %; most of the increase being due to shallow *Mauritia flexuosa* swamps which extend up to hundreds of kilometres from the main rivers (Bayley 1981b). All these potential yield estimates have wide confidence limits which are mainly due to limited data from comparative systems.

For the Manaus fishery Petrere (1982) demonstrated that floodplain area was mainly responsible for attracting fishing effort, but the catch per unit floodplain area was positively related to fishing intensity. The importance of effort, even when it can only be measured in a simple way such as fishermen•km^{-2} has been noted (Welcomme 1979; Bayley 1988) but not always incorporated into comparative models. Accounting for effort indicates maximum yields of 110-160 kg•ha^{-1} for tropical floodplains (Bayley 1988), whereas Welcomme's (1979) norm of 40–60 kg•ha^{-1} reflects the average effort of worldwide data. The maximimum yield estimate corresponds to about 13 fishermen (full and part-time) •km^{-2} of flooded area (Bayley 1985).

The Peruvian data mentioned above indicates an intensity of about 2 fishermen •km^{-2} of floodplain. The average commercial fisherman caught 5.62 t•yr^{-1} whereas average local market/subsistence fishermen caught only 0.564 t•yr^{-1}, primarily because the latter are almost entirely part-time.

Since there are strong socio-economic parallels between the two types of fishery in other countries in the basin, their respective yields (Table 5) were used to estimate overall effort on the basis of the Peruvian data. Total basin estimates were 215 000 local market/subsistence fishermen and 13 600 commercial fishermen, producing an overall intensity of only 1.3 fishermen • km^{-2}.

Comparisons with existing multispecies yield data from other floodplain fisheries will be sensitive to the comparability of the effort measurement. However, fisheries providing data worldwide (Welcomme 1979: Table 4.9) are dominated by artisanal fishermen who are mostly part-time. Bayley's (1988) empirical relationship of yield and effort of tropical floodplain fisheries indicates that to attain the "norm" of 40–60 kg•ha^{-1} would require about 2.5 fishermen • km^{-2}.

These are approximate estimates but are the best available with present worldwide data. The Amazon estimates are conservative due to the flooded area definition, and because the non-Amazon fisheries yield data used for comparison does not include varying proportions of local market/subsistence yields. The predictions need to be conservative, however, because of the large confidence intervals of current methods and our poor understanding of the sustainability of multi-species yields of a given species composition.

Discussion

The foregoing comparative analysis suggests that the total yield could be increased considerably. Bayley (1989) estimated that only 7.4 % of the biological production of commercial-sized fish was realized as yield in the central Amazon floodplain, but there is some "internal consumption" due to an abundance of large piscivores. On the apparently conservative basis of 50 kg•ha^{-1} the Amazon basin could yield 902 000 t•yr^{-1}; but given appropriate markets is it realistic to expect the quality or quantity of effort required?

The type of effort is important. The estimates in this paper suggest that effort would have to be at least doubled, but there is a strong qualification that the high ratio of part-time, local market/subsistence fishermen to commercial fishermen be maintained. Present models are based on artisanal fisheries; these have developed on the basis of small, dispersed fishing units with low capital investment. The effect of increasing effort in the form of large, capital intensive fishing units is difficult to predict. If the drift of people to cities is not counteracted by agricultural development in the várzea, increased yield would be forthcoming from commercial fishermen.

The behavior of the stocks due to more localized and specialized fishing pressure cannot be predicted reliably on the basis of existing comparative data. Traditional fisheries in Africa and Asia have developed largely on the basis of expanding rural populations exploiting a wide range of species. Also, a large yield increase would be at the expense of the present composition of large species presently valuable in the commercial fisheries (Bayley 1981a), which until recently has apparently been constant (B. Merona, pers. comm.).

Agricultural development in the várzea (see Junk 1984b) is probably the only way that artisanal fishing intensity could expand in concert with large commercial operations. However, the question is whether such development would affect aquatic productivity through hydrological alteration, vegetation changes, or chemicals.

The effects on total fisheries production of hydrological alteration due to hydroelectric dams (Bayley 1989) may be more severe than due to deforestation during the next 10–20 years. The well-documented cases in Africa (Bernacsek 1984) in particular the inability of reservoir production to replace losses of floodplain fisheries and agriculture production downstream have been ignored (e.g. Sternberg 1983). It is perhaps fortunate that most projects are sited on the less productive clear and black water rivers. However, their effects on várzea floodplains downstream are unknown, but it is very unlikely that they would enhance fish productivity.

Management Options

Bayley (1981a) discussed options under four broad categories: (a) prohibit commercial fishing permanently; (b) manage the fishery to conserve the present species composition in the yield; (c) manage the fishery on a high-yield basis; and (d) do nothing (except monitor catch and effort). Any management decision must take into account the cost of education, which is considerable in an area of poor facilities and dispersed populations.

Because of the size of the basin and extensive areas with sparse human population, (a) is possible in selected areas which can be controlled. There are three effectively protected areas (Bayley 1989), two of which contain várzea, but they are limited in size. This option could maintain all but the larger fish undergoing extensive migrations, such as *Colossoma* and *Brachyplatystoma* spp. under relatively unexploited conditions in a naturally forested environment. This option is desirable not only from the conservation point of view, but to enable long-term studies on dynamic characteristics which are difficult with changing exploitation and environmental regimes. To some extent commercial fisheries would benefit from increased catch per unit effort of large, valuable species in areas adjacent to protected zones.

Option (b) was not considered feasible (Bayley 1981a) because of the prohibitive cost involved in maintaining the existing high yields of the large species such as *Colossoma macropomum*, *Brachyplatystoma* spp. and *Arapaima gigas* using traditional methods such as gear, fish size, or catch limitations. It was predicted that these species would decline. Since then, *C. macropomum* yield has apparently declined (SUDEPE 1985), but due to lack of appropriate effort data in recent years, the reason for the decline is not clear. However, the aforementioned decline of mean weight despite the increase in distance fished from Manaus for *C. macropomum* suggests that overexploitation of this species has occurred.

Providing that the hydrological regime, water quality, and forests are protected along large reaches of major rivers and tributaries and that massive rural colonization of riverbanks does not occur, we consider it very unlikely that large species could be exploited to biological extinction. In this respect, the flooded forest not only provides food, but is at least as important in providing protection from fishing gear.

The depression of stocks of large species is the inevitable adjustment of species compositions resulting from a multigear, multispecies fishery supplying diverse markets. This "fishing-up" process has been documented in other fisheries (Welcomme and Henderson 1976; Welcomme 1979). Outside National Parks, the question of if and how to control the exploitation of certain species is an economic one. Unenforceable regulations, such as the size limit and closed season for *Arapaima*, remove our ability to assess the results of management because of the resulting impossibility of obtaining reliable catch and effort data. The cost of effective education and enforcement which imposes limits on gear or catch would amount to a significant subsidy to the fishery. Probably the only economic method which might arrest the "fishing-up" process at a position more desirable than attained by market forces is to periodically prohibit fishing from certain strategic areas (pulse fishing). This has recently been tried in Brazil on the R. Purus (M. Goulding, pers. comm.) but the results are not known.

Areas near cities such as Manaus, Iquitos, Pucallpa, and Santarem are approaching a level in which the high-yield option (c) would be preferable (Bayley 1981a; Ribeiro 1983). Larger species are depressed, but a larger diversity of fish species is caught. Smaller species of lower market value can be profitably extracted such as Prochilodontidae, Curimatidae, Anostomidae, Hemiodontidae and *Triportheus* spp. Since the late 1970's the prices of prime quality species including *Colossoma, Cichla* and *Plagioscion* have exceeded that of chicken (Goulding 1983). The lower socioeconomic groups in the cities depend on these more intense fisheries providing smaller, cheaper species, and to attempt to manage these areas in order to optimize yields of larger, prime quality species would be unwise even if it were to succeed.

These fisheries are only intense by present Amazon standards. For example in the várzea within 200 km of Manaus the yield is only 19 kg•ha^{-1}. There are numerous, medium-sized species which are underexploited because of either market or preservation problems. These problems cannot be overemphasized. The human population is far more selective than the combined effects of the wild piscivores. It is probable that these high-yield fisheries can be predicted and managed more effectively when a larger number of species above a certain size are exploited. Exploitation of piscivorous fish can increase the available production of prey species, for example. There is a need for research and development of improved preservation and packaging of alternate fish species, and the development of their markets. There will be some failures, but an advantage in this area is that there are many species. In the future there will continue to be adaptation to new species, but without investment in product and market development these changes will only tend to occur after long periods of depressed yields of preferred species.

The contrasts between the local market/subsistence and commercial fisheries described earlier are highlighted by the conflicts, often violent, which occur in Brazil and Peru. Some areas are unofficially closed to commercial fishermen. The city-based professionals work under very different economic circumstances. They require high-valued catches per unit time of certain species and their purveyors can afford expensive gear (lampara and beach seines, large gillnets), transport and supplies to achieve this.

Some of the local fishermen sell their more valuable species to visiting commercial boats, or even work temporarily for the visiting fishermen. However, the riparian population consists primarily of farmers many of whom fish for limited periods each day, often catching sufficient to be able to sell excess catch locally. They are accustomed to a high catch per effort for desirable species due to low fishing intensity. In contrast, the commercial fishermen need to operate at a higher exploitation rate, which lowers the local stock sizes of the desired species which makes life more difficult for the local fishermen. Moreover, they are not concerned about local equilibrium of stocks, since they can cover very large areas. Neither side can be blamed. If all the local fishermen were granted sole fishing rights there would be catastrophic shortages of protein in the cities. A compromise solution must be accompanied by sound arguments if it to succeed, but this requires data which are at present insufficient.

In conclusion, although there is room for expansion in the fishery, the socio-economic circumstances need to dictate which is the more desirable mixture of fisheries and species. Since it is impossible to manage most species separately, the choice is limited to a single spectrum which ranges from a limited yield of a few large, highly valued species to a high yield of many smaller species. This spectrum could vary somewhat by improved preservation and packaging of new species or long term changes in market preferences.

We recommend a mixture of options. Near large population centers the high yield, multispecies option (c) should be encouraged by developing products and markets for new species and removing unenforceable regulations. Yield, effort, and species composition should be monitored carefully, in particular if the expansion is based on increased capital-intensive operations. Low capital, artesanal operations should be encouraged. Conversely, option (a) should be applied to selected, distant areas. They should be protected completely if the human population is negligible, or otherwise reserved for local artesanal fishing interests. Intermediate areas might be considered for pulse fishing with appropriate monitoring.

Research Needs

A detailed knowledge of the life histories of fish species in the Amazon would do little to improve management, even if the fisheries could be suspended for a few hundred years until the studies were completed. However, selective studies on migration patterns and the determination of stocks or populations would be useful for fisheries management. This could not only benefit single stock approaches, but provide better criteria for stratifying the basin into units for comparative analyses.

It is unlikely that improved ecological theory will lessen the need for better quality data on the various fisheries. Southeast Asian marine fisheries have relatively good quantitative data by tropical, multispecies standards, but the overriding need is still for more date for empirical solutions (Pauly and Murphy 1982).

The glaring omission from Amazon fisheries data is regular statistics on catch, effort and species composition from the local market/subsistence fisheries which account for 60 % of the yield. As described in this paper it is possible to obtain useful statistics from this dispersed fishery without depending on infrequent injections of foreign aid.

The commercial fisheries data are by no means adequate. The recording and data treatment system set up for the Manaus fishery has not been continued, resulting in biased yield estimates and inferior effort statistics in recent years. It is pointless to spend money on management, education, or attempts to settle disputes without generally accepted statistical records.

It is not intended to belittle the importance of biological studies which are necessary for improving our understanding of the system in the long term, but rather to emphasize the major requirements for maintaining or expanding amazon fisheries. Lessening the importance of the fisheries will remove a major defense against alternative exploitations which will be much less friendly to the environment and its residents.

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References

ARAUJO-LIMA, C. A. R. M., AND E. HARDY. 1985. A alimentação dos alevinos do jaraquí escama grossa. Abstract in Resumos de Zoología, XIII Congresso Brasileiro, Universidade Federal de Mato Grosso, Cuibá — MT, Brazil.

AZEVEDO DE, P., M. V. DIAS, AND B. B. VIEIRA. 1938. Biología do saguiró. Mem. Inst. Oswaldo Cruz Rio de J. 33: 482–553.

BARTHEM, R. B, 1981. Considerações sobre a pesca experimental com redes de espera em lagos da Amazônia Central. M.Sc. thesis, INPA, Manaus, Brazil. 84 p.

1985. Occorência, distribuicão e biología de peixes da Baía de Marajó, Estuário Amazônico. Boletim do Museu Paraense Emilio Goeldi, Zoología (Belém, Brasil) 2: 49–69.

BAYLEY, P. B. 1981a. Fish yield from the Amazon in Brazil: comparisons with African river yields and management possibilities. Trans. Am. Fish. Soc. 110: 351–359.

1981b. Características de inundación en los rios y áreas de captacón en la Amazonia Peruana: una interpretación basada en imagenes del 'LANDSAT' e informes de 'ONERN'. Inst. Mar. Peru(Callao) Inf. 81: 245–303.

1981c. Evaluación de la situación actual del proyecto FAO-PER/76/022 en Iquitos, y recomendaciones para el mejoramiento de los procedimientos de limnología y biología pesquera. Inst. mar. Peru(Callao) Inf. 81: 209–242.

1983. Central Amazon fish populations: biomass, production and some dynamic characteristics. Ph. D. thesis, Dalhousie University, Halifax, Nova Scotia, Canada, 330 p.

1984. Fisheries and fish culture potential in the Alto Huallaga region in Peru in the context of national trends in fish production. IRI Research Institute Inc. report (contract to AID, US Government).

1985. Fish resources, p. 137–140. *In* Environmental Profile of Paraguay. International Institute for Environment and Development (IIED), Washington, USA.

1986. Fisheries assessment in Panama reservoirs. Report to FAO project TCP/PAN/2303 (Ma), Rome 19 p.

1988. Accounting for effort when comparing tropical fisheries in lakes, river-floodplains and lagoons. Limnol. Oceanogr. 33: 963–972.

1989. Aquatic environments in the Amazon basin, with an analysis of carbon sources, fish production, and yield, p. 399-408. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Bayley, P. B., and J. C. Moreira. 1980. Preliminary interpretations of aquatic resources in the Central Amazon Basin using LANDSAT multispectral imagery, p. 861-868. *In* J. I. Furtado [ed.] Tropical ecology and development. Proceedings of the Vth International Symposium of Tropical Ecology. International Society of Tropical Ecology, Kuala Lumpur.

Bazigos, G. 1974. the design of fisheries statistical surveys — inland waters. FAO Fish. Tech. Pap. 133: 122.

Bernacsek, G. M. 1984. Guidelines for dam design and operation to optimize fish production in impounded river basins. CIFA Tech. Pap. 11: 98.

Böhlke, J. E., S. E. Weitzman, and N. A. Menezes. 1978. Estado actual da sistemática dos peixes de água doce da América do Sul. Acta Amazonica 8: 657-677.

Braum, E., and W. J. Junk. 1982. Morphological adaptation of two Amazonian Characoids (Pisces) for surviving in oxygen deficient waters. Int. Revue ges. Hydrobiol. 67: 869–886.

Carvalho, F. M. 1983. Marcação de peixes na região do Janauacá Manaus(AM). Acta Amazonica 13: 707–708.

Castillo, O. R. G. 1978. Pesca: artes e métodos de captura industrial no estado do Pará Brasil. BFACP (Belém, Brazil) 10: 93–112.

Chapman, D. W.. 1981. Evaluación de capturas en el Lago Titicaca y en el Rio Amazonas en el Peru. Inst. Mar. Peru (Callao) Inf. 81: 49–108.

Eckmann, R. 1985. The fisheries situation in the Peruvian Amazon region. Anim. Res. Dev. 21: 59–86.

ENCA. 1972. Encuesta nacional de comercialización de alimentos. Ministerio de Alimentación, Lima, Peru.

Fittkau, E. J., U. Lemler, W. S. Junk, F. Reiss, and G. W. Schmidt. 1975. Productivity biomass, and population dynamics in Amazonian water bodies, p. 289–311. *In* Z. B. Golley and B. Medina [ed.] Tropical ecological systems. Springer-Verlag, New York, NY.

Gaviria, A. 1980. Consumo de carne de monte por los Campas del Pichis. Proyecto CIPA/COTESU (unpublished report), Puerto Bermúdez, Peru.

Goulding, M. 1979. Ecología da pesca do Rio madeira. Conselho Nacional de Desenvolvimento Científico e Tecnológico (INPA), Manaus, Brazil.

1980. The fishes and the forest. California University Press.

1981. Man and fisheries on an Amazon frontier. Dr. W. Junk Publishers, The Hague.

1983. Amazonian fisheries, p. 189–210. *In* E. F. Moran [ed.] The dilemma of Amazonian development. Westview Press, Boulder, Colorado.

Guerra, H. F., V. F. Montreuil, and M. C. Villacorta. 1981. Avances del programa de la evaluación de recursos pesqueros en la Amazonia peruana. COPESCAL (Comisión de Pesca Continental para mérica Latina), unpublished document, Colombia.

Hanek, G. [ed.]. 1982. La pesquería en la amazonia peruana: presente y futuro. Documento Técnico de Pesca, FAO, Rome.

IBGE. 1981. Sinopse preliminar do censo demográfico: IX recenseamento geral do Brasil — 1980. Fundação Instituto Brasileiro de Geografía e Estatística, Rio de Janeiro, Brazil.

IMARPE. 1972. Encuesta de consumo de pescado. Instituto del Mar del Peru/Programa bilingüe, Lima, Peru.

INE. 1982. Boletín de divulgación no. 01-83: Población. Instituto Nacional de Estadística, Lima, Peru.

Johns, P. M. 1982. A key and proposed revisions to the characoid fishes of the Family Hemiodontidae from the Central Amazon. Honours thesis, Department of Biology, Dalhousie University, Canada. 49 p.

Junk, W. J. 1983. Ecology of swamps on the middle Amazon, p. 269–294. *In* A. J. P. Gore [ed.] Mires: swamp, bog, fen and moor, B. Regional studies. Elsevier, Amsterdam.

1984a. Ecology, fisheries and fish culture in Amazonia, p. 443–476. *In* H. Sioli [ed.] The Amazon (Monographiae biologicae, Vol. 56). Dr. W. Junk, Dordrecht, Netherlands.

1984b. Ecology of the várzea, floodplain of Amazonian whitewater rivers, p. 215–244. *In* H. Sioli [ed.] The Amazon (Monographiae biologicae, Vol. 56). Dr. W. Junk, Dordrecht, Netherlands.

Junk, W. J., F. M. Soares, and F. M. Carvalho. 1983. Distribution of fish species in a lake of the Amazon river floodplain near Manaus (Lago Camaleão), with special reference to extreme oxygen conditions. Amazoniana 7: 397–431.

Kapetsky, J. M. 1981. Evaluación del programa de IMARPE para la evaluación pesquera en la Amazonia. Inst. Mar. Peru(Callao) Inf. 81: 111–170.

Klammer, G. 1984. The relief of the extra-Andean Amazon basin, p. 47–84. *In* H. Sioli [ed.] The Amazon (Monographiae biologicae, Vol 56). Dr. W. Junk, Dordrecht, Netherlands.

Kramer, D. L., C. C. Lindsey, G. E. E. Moodre, and E. D. Stevens. 1978. The fishes and the aquatic environment of the Central Amazon Basin, with particular reference to respiratory patterns. Can. J. Zool. 56: 717–729.

Lagler, K. F., J. M. Kapetsky, and D. J. Stewart. 1971. The fisheries of the kafue river flats, Zambia, in relation to the Kafue George Dam. University of Michigan Technical Report. FAO, Rome, FI:SF/ZAM 111: 161 p.

Lowe-McConnell, R. H. 1975. Fish Communities in Tropical Freshwaters. Longman, London.

Lowe-McConnell, R. H. and G. J. Howes. 1981. Pisces, p. 218–229. *In* S. H. Hurlbert, G. Rodriguez, and N. D. Santos [ed.] Aquatic Biota of Tropical South America. San Diego State University, San Diego, USA.

Pauly, D., and G. I. Murphy [ed.]. 1982. Theory and management of tropical fisheries. ICLARM Conference Proceedings 9. International Center for Living Aquatic Resources Management, Manila, Philipines and Division of Fisheries Research, Commonwealth Scientific and Industrial Research Organization, Cronulla, Australia.

Pedini, M. F. 1981. Evaluación de los proyectos de acuicultura en el Peru y determinación de las bases para su planeamiento y desarrollo. Inst. Mar. Peru(Callao) Inf. 82: 41–146.

Petrere, M., Jr. 1978a. Pesca e esforço da pesca no Estado do Amazonas II Locais, aparelhos de captura e estatísticas de desembarque. Acta Amazonica 8: 1–54.

1978b. Pesca e esforço de pesca no estado do Amazonas. I. Esforço e captura por unidade de esforço. Acta Amazonica 8: 439–454.

1982. Ecology of the fisheries in the river Amazon and its tributaries in the Amazonas State (Brazil). Ph.D. thesis, University of East Anglia, U.K. 96 p.

1983a. Relationships among catches, fishing effort and river morphology for 8 rivers in Amazonas State (Brazil), 1976–1978. Amazoniana 8: 281–296.

1983b. Yield per recruit of the tambaqui, *Colossoma macropomum* Cuvier, in the Amazonas state, Brazil. J. Fish. Biol. 22: 133–144.

1985a. Migraciones de peces de agua dulce en America Latina: algunos comentarios. COPESCAL Doc. Ocas. 1: 17.

1985b. A pesca comercial no Rio Solimões-Amazonas e seus afluentes: análise dos informes do pescado desembarcado no Mercado Municipal de manaus (1976–1978). Ciência e Cultura (Brazil) 37: 1987–1999.

RADAMBRASIL. 1976. Projecto Radambrasil: Levantamento de recursos naturais (15 volumes). Ministerio das Minas e Energia, Rio de Janeiro, Brazil.

Ribeiro, M. C. L. B. 1983. As migrações dos jaraquis (Pisces, Prochilodontidae) no Rio Negro, Amazonas, Brasil. M.Sc. thesis, INPA, Manaus, Brazil. 192 p.

Ricker, W. E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30: 409–434.

Roberts, T. R. 1972. Ecology of fishes in the Amazon and Congo basins. Bull. Mus. Comp. Zool. Harv. 143: 117–147.

Robinson, M.A. 1984. Trends and prospects in world fisheries. FAO Fish. Circ. 772: 25.

Shrimpton, R., R. Giugliano, and N. M. Rodrigues. 1979. Consumo de alimentos e alguns nutrientes em Manaus. Acta Amazonica 9: 117–141.

Sioli, H. 1966. General features of the delta of the Amazon, p. 381–390. *In* Scientific Problems of the Humid Zone Deltas and Their Implications. Proceedings, Dacca Symposium, UNESCO.

1984. The Amazon and its main affluents: hydrography, morphology of the river courses, and river types, p. 127–166. *In* H. Sioli [ed.] The Amazon (Monographiae biologicae, Vol. 56). Dr W. Junk, Dordrecht, Netherlands.

Smith, N. J. H. 1979. A pesca no Rio Amazonas. Conselho Nacional de Desenvolvimento Científico e Tecnológico (INPA), Manaus, Brazil.

1981. Man, Fisheries and the Amazon. Columbia University Press, New York, NY.

Sternberg, R. 1983. Hydroelectric energy, repressed demand and economic change in Amazonia. Acta Amazonica 13: 371–391.

SUDEPE. 1985. Superintêndencia do Desenvolvimento da Pesca: Relatorio da segunda Reunião do Grupo de Trabalho e Treinamento (GTT) sobre avaliação de Estoques, in Tamandaré, PE. Série Documentos Técnicos No. 34. Brasilia, Brazil.

Verissimo, J. 1895. A pesca na Amazônia. Livraria Clássica de Alvez, Rio de Janeiro, Brazil.

Welcomme, R. L. 1975. The fisheries ecology of African floodplains. CIFA Tech. pap. 3:51.

1976. Some general and theoretical considerations on the fish yield of African rivers. J. Fish. Biol. 8: 351–364.

1979. Fisheries ecology of floodplain rivers. Longman, London.

1985. River fisheries. FAO Fish. Tech. Pap. 262: 330.

Welcomme, R. L., and H. F. Henderson. 1976. Aspects of the management of inland waters for fisheries. FAO Fisheries Technical Paper 161: 36.

Werder, U., and U. Saint-Paul. 1979. Experiencias de alitação com tambaquí (*Colossoma macropomum*), pacu (*Mylossoma* sp.), jaraquí (*Semaprochilodus theraponura*) e matrinchã (*Brycon melanopterum*). Acta Amazonica 9: 617–619.

Worthmann, H. O. 1982. Aspekte der Biologie zweier Sciaenidenarten, der Pescadas *Plagioscion squamosissimus* (Heckel) und *Plagioscion montei* (Soares) in verschiedenen Gewässertypen Zentralamazoniens. Ph.D. thesis, University of Kiel, West Germany. 176 p.

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Aquatic Environments in the Amazon Basin, with an Analysis of Carbon Sources, Fish Production, and Yield

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Abstract

BAYLEY, P. B. 1989. Aquatic environments in the Amazon Basin, with an analysis of carbon sources, fish production, and yield, p. 399–408. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The principal aquatic environments of the basin are described. A carbon flow analysis in a floodplain in the center of the basin indicated that macrophytes, forest litter, phytoplankton, and periphyton contributed carbon in the proportions 69, 24, 5.4, and 1.5 %, respectively, in an area where 54 % of the estimated original flooded forest remains. The estimated quantity of carbon contributed by the river channel was negligible compared with the amount photosynthesized within the floodplain. Fish production (including a small contribution by prawns) was 1.03 % of total photosynthesized carbon in the floodplain. It is hypothesized that fish production utilized primary production efficiently, and that all carbon sources are necessary qualitatively and quantitatively. However, the fish yield was only 2.7 % of fish production, and only 7.4 % of the production of fish of market size. This low efficiency was attributed to very high predation by piscivores and underutilization of many fish species. The dependence of fish production on the preservation of the flooding regime and the sources of primary production is stressed.

Résumé

BAYLEY, P. B. 1989. Aquatic environments in the Amazon Basin, with an analysis of carbon sources, fish production, and yield, p. 399–408. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

On décrit les principaux environnements aquatiques du bassin versant de l'Amazone. Une analyse du cycle du carbone d'une plaine inondable du centre du bassin versant a révélé que la production de carbone par les macrophytes, la litière, le phytoplancton et le périphyton se situe à 69 %, 24 %, 5,4 % et 1,5 % respectivement dans une région où il reste environ 54 % de la fôret inondée originale. La quantité estimative de carbone provenant du lit du fleuve est négligeable par rapport à la quantité produite par photosynthèse dans la plaine inondable. Les poissons produisent 1,03 % (y compris une faible production par les crevettes) du volume total de carbone photosynthétisé dans la plaine inondable. On formule l'hypothèse que la production par les poissons est basée sur l'utilisation efficace de la production primaire et que toutes les sources de carbone sont nécessaires aux niveaux qualitatif et quantitatif. Toutefois, le rendement des poissons ne s'élevait qu'à 2,7 % de la production par les poissons et ne représentait que 7,4 % de la production de poissons de taille commerciale. On attribue cette faible efficacité au niveau élevé de prédation exercé par les piscivores et la sous-utilisation de nombreuses espèces. On souligne l'importance de la dépendance de la production piscicole sur la permanence du régime de crues et des sources de production primaire.

This paper describes the aquatic environment of the Amazon basin with emphasis on the most productive areas. These areas are floodplain habitats influenced by the hydrology and chemistry of the major rivers originating in the Andes. They are responsible for important food fisheries in the basin (Bayley and Petrere 1989). What is the trophic basis of the fish production supporting these fisheries? What environmental changes could alter fish production? In this paper a carbon flow analysis from the central Amazon floodplain, which compares the major sources of carbon with the quantities manifested as fish production and yield, addresses these questions. Bayley and Petrere (1989) describe the fisheries and life histories of major taxa, estimate present and potential yields throughout the basin, and discuss management options given no change in the environment.

The Environment

The Amazon basin covers 7 050 000 km^2 including the R. Tocantins (Sioli 1984), of which about 58 % lies in Brazil, 16 % in Peru, 10 % in Bolivia, and the remainder in Colombia, Ecuador, and Venezuela (Fig. 1). Most of the basin has a flat topography, which is a pediplain of non-flooded Tertiary sediments at less than 200 m above sea level, defined as "terra firme". However, this vast pediplain is not flat in the immediate vicinity of tributaries where slopes can be significant. The Andes to the west and lower ranges to the north and south surround this pediplain.

The climate was classified as hot humid or superhumid by Nimer (1977). The annual average temperature lies between 24 and 26°C with little seasonal variation. However, between June and October it can drop to 16°C because

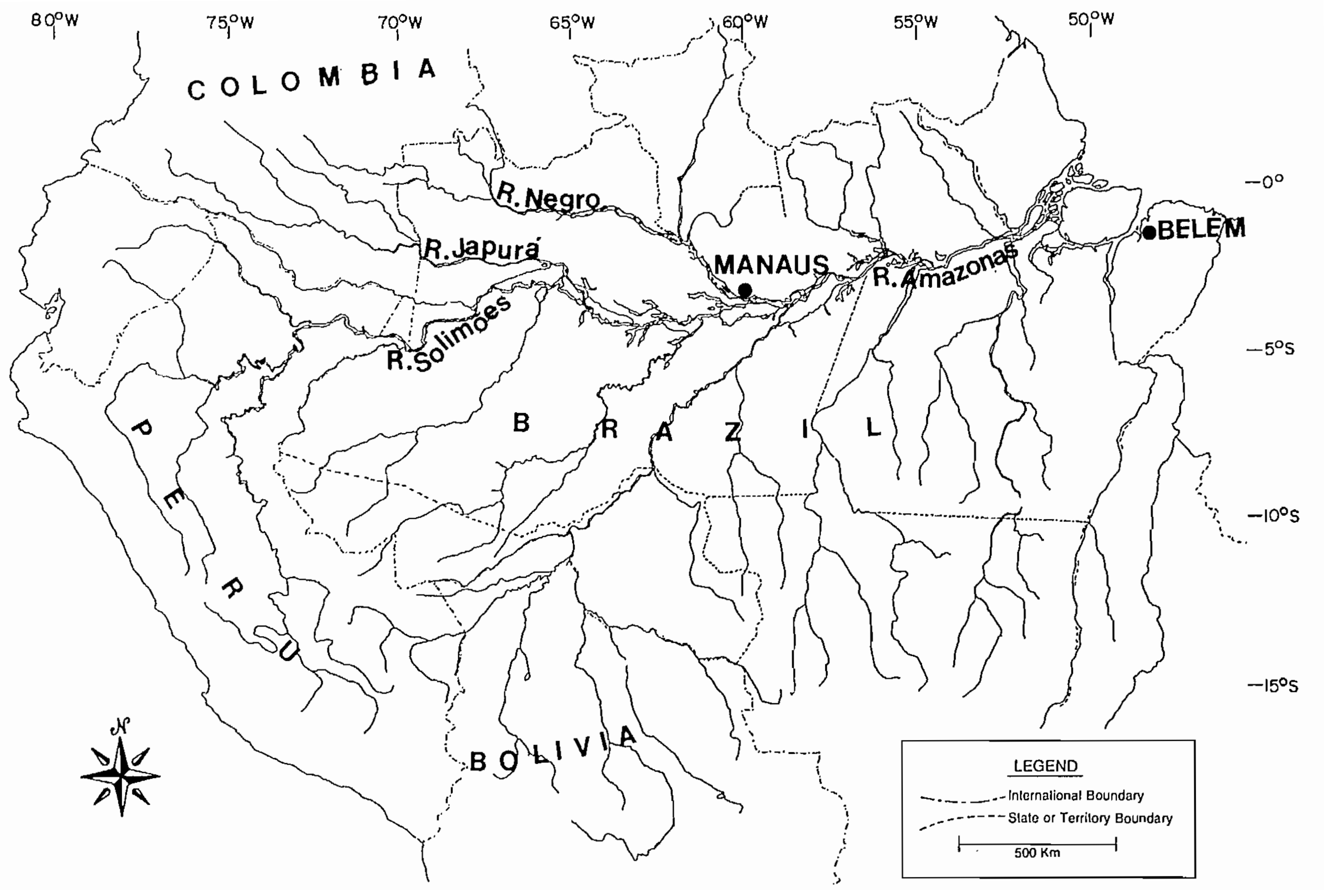

FIG. 1. Amazon basin with major rivers.

of the polar anticyclone which comes over the Andes from the south of Chile. This phenomenon, known as "friagem", can cause fish mortality locally due to turnover of stratified floodplain lakes, which results in deoxygenation and hydrogen sulphide throughout the water column (Brinkmann and Santos 1973).

The climate in the Amazon Basin is strongly influenced by atmospheric dynamics associated with the intertropical convergence. The portion of the basin in the southern hemisphere is about six times larger than the northern portion. Annual rainfall increases from 1.6 $m \cdot yr^{-1}$ in the lower reaches to 3.5 $m \cdot yr^{-1}$ in Iquitos, Peru. Higher values occur close to the Andes. Most rain falls during the austral summer in the south, and during the boreal summer north of the equator. This alternation of rainfall combined with a large, well-forested basin produces a smooth flooding regime in the main channel (Fig. 2), with only about 4 months during the year when water is confined to the main channels or floodplain lakes, and at least a 7-month period of expanded flooded area in the central basin. Salati and Vose (1984) discuss the importance of the forest in maintaining the present hydrological regime. The evapotranspiration of the forest, in combination with the Andes forming a barrier to the prevailing easterly winds, causes recycling of 50 % of the precipitation within the basin.

The maxima and minima of the lower R. Negro hydrograph (Fig. 2) correspond closely to the levels in the R. Solimões-Amazonas floodplain about 30 km from Manaus (Schmidt 1973a). This is due to the backing up of the lower R. Negro by the R. Solimões-Amazonas. Annual minimum to maximum river stage differences range from 5.5 to 14.1 m and averaged 10.0 m (±1.9 SD) in Manaus from 1902–80 (Manaus Port Authority data). They varied from 5.2 to 6.4 m at Parintins on the lower R. Amazonas from 1971–74 (Centrais Elétricas Brasileiras S.A., unpublished data). At Iquitos, the average amplitude was 7 m, and the maximum 12.5 m from 1962–81 (Iquitos Port Authority data in Hanek 1982). Consequently, there is not a uniform trend of increasing amplitude proceeding upstream.

At Manaus the annual maximum water levels are more variable than the minimum levels. Since greater flooding is associated with higher productivity, and low levels are associated with higher mortality (Welcomme and Hagborg 1977; Welcomme 1979), the latter effect would be expected to have a greater influence on year to year variation in fish production and yield. There is also a trend in mean levels: since the mid 1960's the minimum has averaged about 2 m above that of the period 1902–64, with no corresponding trend in the maximum flood levels (Bayley 1983).

Limnology

Wallace (1853) and Sioli (1964) followed the original classification by indigenous people of classifying Amazonian rivers into three types. The following brief description uses information from Gibbs (1967) and Hanek (1982). More detailed geochemical data can be found in Stallard (1980). Dissolved salts are dominated by those of terrestrial

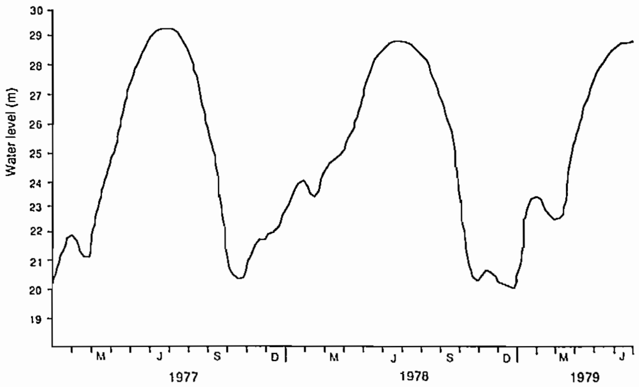

FIG. 2. Daily water levels at Manaus.

origin (Stallard and Edmond 1981).

Typical "white water" rivers have high turbidity with a Secchi transparency of 4–50 cm, near neutral pH, and specific conductances of 50–380 μmhos•cm^{-1}. They are typified by major rivers originating in the Andes such as the Amazon itself. The higher salinities occur nearer the Andes, and decrease downstream due to the effects of lower conductivity tributaries from the pediplain and the granitic shield to the north and south. Conductivities of up to 460 μmhos•cm^{-1} also occur seasonally in the associated floodplain lakes (Bayley 1983).

"Clear water" rivers, with transparencies of 100–400 cm, but variable chemistry, are typified by tributaries from the south in the lower basin such as the R. Tapajos. "Black water" rivers have a dark red-brown hue owing to humic and fulvic acids, transparencies of 60–200 cm, low pH, typical conductivities of 5–15 μmhos•cm^{-1}, and virtually no inorganic suspended solids. The R. Negro is the largest example.

This classification is not perfect due to seasonal changes in some rivers (Sioli 1984). For example, some rivers in Peru, such as the R. Tigre, appear to be "black" but have conductivities in the 20–40 μmhos•cm^{-1} range (L. Azabeche, pers. comm.; Azabeche et al. [1981] in Hanek [1982]).

It is well accepted that white waters are chemically the richest (Sioli 1964; Fittkau et al. 1975), being associated with higher dissolved nutrients. The attrition of the Andes controls the geochemistry of the Amazon River (Gibbs 1967). Clear water rivers have their catchment area on the less rugged relief of the Brazilian and Guyanian shields. Black water rivers drain from flatter regions. Although there is general agreement on black water being linked to a special type of soil (bleached white sands) or vegetation ("campina"), the relative importance of the two factors is widely disputed (Janzen 1974).

The main biological production and food chains important to the fish populations occur in the white-water floodplains or "várzea" (Fittkau et al. 1975; Bayley 1983; Junk 1984a). The várzea was formed by the deposition of clay and silts from the river during and after the Quaternary period, filling valleys formed by the sea level depression during the last ice age (Irion 1984; Klammer 1984). The width of the floodplain varies along the Amazon River and is widest in lower Amazonas State. However, tributaries in Bolivia and Peru have very extensive flooding. Floodplain area determinations throughout the basin are presented in Bayley and Petrere (1988). The productive, várzea floodplains amount to 2.6 % of the basin area. This is higher than typical worldwide values which are usually less than 1 % (Welcomme 1979). Human settlement in the basin is densest in the várzea floodplain (Sioli 1973) because the soil is best for growing cattle and crops, and many fisheries occur within (Petrere 1982) or result from the biological production there (Bayley 1983).

The várzea lakes follow the regimen of the main river, being invaded by its waters in the rainy season and partially draining to the main channel in the dry season. In the middle and lower reaches of the white water rivers where the major floodplains exist, most of the total lake area is connected to the river via channels for more than 10 months per year, but a number of small lakes and permanent swamps are disconnected for longer periods (Junk 1983). In upstream reaches of some tributaries, such as the R. Madeira and R. Negro, a larger proportion of floodplain waters are separated from the river for longer periods (M. Goulding, pers. comm.).

The "terra firme lake" or "ria-lake" (Irion 1984), is also an important fish biotope. These lakes are drowned valleys formed by lower sea levels, but have not filled with sediment because of the absence of white water rivers. However, the mouths of many ria-lakes are dammed by white water rivers or the associated várzea waters, and are influenced by them. The shorelines of these lakes and those of the numerous black and clear water tributaries have narrow floodplains covered by forest defined as "igapó", such as that bordering in the lower R. Negro and its associated lakes. Igapó comprises an important feeding area for many fish species (Goulding 1980).

The estuary of the Amazon is another important biotope with a complex hydrology (Sioli 1966) and a great variability in its salinity, which is higher in the dry season. The estuary discharges 6300 km^3•yr^{-1} of freshwater and 9.3×10^8 t•yr^{-1} of sediments (Meade et al. 1979) into the sea, representing 20 % of the total freshwater discharge (Gibbs 1970) and 7 % of the sediment transport (Milliman and Meade 1983) of all rivers worldwide. The contact zone between the river and the sea is displaced 200 km annually.

Protected Areas

Only two small várzea areas are effectively protected in the basin: The Manu National Park in Peru and the Cuniá reserve near Porto Velho, Brazil. The latter protects the várzea associated with the R. Cuniá, an affluent of the R. Madeira. The Manu park protects the R. Manu and its floodplain. However, its limited size and its position near the Andes upstream of the upper R. Madeira falls exclude a number of large migratory fish species from its endemic fauna (S. K. Robinson, pers. comm.). The Pacaya-Samiria Reserve, also in Peru, includes a large várzea floodplain adjoining the R. Ucayali, but it is not effectively controlled. The Anavilhanas Reserve protects the archipelago of about 300 islands covered with igapó forest in the lower R. Negro.

Modifications

No modifications have occurred so far which have apparently affected the Amazon hydrology on a large scale. However, our ability to detect changes is restricted by the sparse distribution of river level and rain gauges, and by the complex hydrology of floodplains. Gentry and López-Parodi (1980) detected a change in the hydrological regime in the Peruvian Amazon which was independent of the rainfall pattern, and associated this change with deforestation upstream, but this was questioned by Nordin and Meade (1982). Deforestation on the eastern Andean slopes of high rainfall, in particular in Peru and Bolivia where it is accelerating, will probably cause greater seasonal flooding despite a predicted basinwide reduction in precipitation (Salati and Vose 1984).

Deforestation in flooded forest biotopes is variable. In the várzea along 205 km of the R. Solimões-Amazonas near Manaus 54 % of the original flooded forest remains (Bayley 1983). In general, this decreases downstream and increases upstream, except near large riverine cities and Andean colonization projects. Riverine populations are thinly dispersed along the black and clear water rivers and deforestation in the associated igapó forest appears to be minimal.

There are few man-made lakes in the basin. Apart from small hydroelectric dams in the Peruvian and Bolivian Andes, there are three completed lakes in the lower basin: Tucururi on the R. Tocantins (2 430 km^2), and Paredõ near Belém and Curuá-Una near Santarem of somewhat less than 100 km^2 each (Junk and Mello 1987). Vieira (1982) reported that after construction of Curuá-Una fish species richness was reduced and the proportion of predatory species increased. Eight additional hydroelectric power impoundments up to about 6 100 km^2 in area are under construction or planned (Junk 1984b; Junk and Mello 1987).

Production and Carbon Flow

To what extent is fish production dependent on the various sources of photosynthesized carbon? Are all the sources

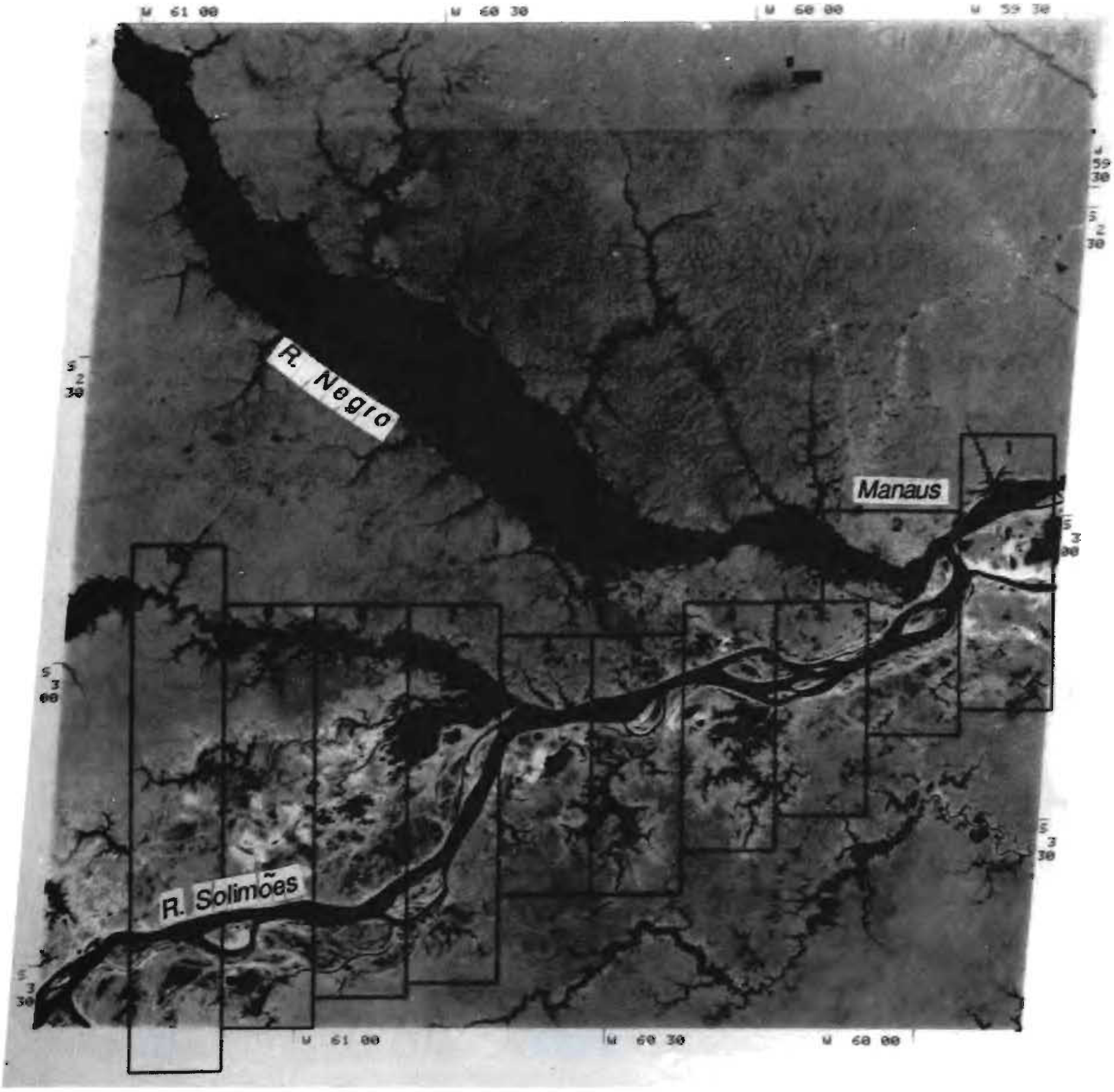

FIG. 3. LANDSAT near infrared image at low water, including quadrats 2–10 which enclosed study area. Data from another image was used to complete analysis of quadrat 10. (East–west extent of image: 184 km^2).

essential? Could we predict fish productivity or yield from primary productivity? Qualitative data, including fishermen's information, have long indicated the importance of tree fruits (Goulding 1980), macrophytes and seeds (Almeida 1980; Paixão 1980; Carvalho 1981; Santos 1981; Soares et al. 1986) to individual fish species. Recent data of carbon flow permit a more quantitative response to these questions with respect to the várzea, which is clearly responsible for a major part of the fish yield. It is stressed there are many other systems within the basin not associated with the major fisheries, such as clear water savanna streams, which have quite different vegetation characteristics (Junk and Howard-Williams 1984).

To compare carbon flows from different sources, it is necessary to account for areas associated with each component and their seasonal changes. In addition, an area should be large enough to be representative of a fish yield so that net emigration over an annual period can be considered negligible. One of the most intensively fished and studied várzea areas in the basin, comprising a maximum flooded area of 5 330 km^2 on the R. Solimões between the confluences of the R. Negro and R. Purus (Fig. 3), was ideal for this purpose. This area was analysed for proportions of major aquatic vegetation and water types using multispectral analysis combined with ground truth data at high and low water periods (Bayley and Moreira 1980; Bayley 1983).

Fish yield, fish production and phytoplankton production were compared in the várzea in the Central Amazon (Bayley 1984; Fig. 3). Annual biological production of fish and decapods was estimated on the basis of 600 samples taken at 2–wk intervals throughout the annual cycle. Twenty-three calibrations of the fishing gear efficiency allowed biomass density to be estimated from catch data (Bayley 1983). Production was estimated on the basis of biweekly biomass densities by size and species group and instantaneous growth rates calculated from modal length progressions of 14 key species. Growth rates were a function of individual size, maximum size of species, and hydrological season (Bayley 1983).

Only about 10 % of a total 'fish' production of 28 g $C \cdot m^{-2} \cdot yr^{-1}$ (1 % of which was *Macrobrachium* spp.) could, hypothetically, be supported by a mean phytoplankton C14 productivity of 290 g $C \cdot m^{-2} \cdot yr^{-1}$ (Schmidt 1973b) if only one intermediate trophic level of zooplankton with transfer efficiencies of 10 % were assumed (Fig. 4). The estimate of fish production is conservative because fish under 15 mm long were excluded. Also, a simple trophic linkage was presumed with no loss of phytoplankton due to precipitation and permanent burial, which can be significant in várzea lakes (Devol et al. 1984). A more complex, realistic system would require more phytoplankton to support a given fish productivity. It was therefore concluded that phytoplankton only accounted for a small part of the photosynthesized carbon required to support fish production. Recent estimates of várzea lake phytoplankton productivity (214 g $C \cdot m^{-2} \cdot yr^{-1}$ [C14] calculated from Devol et al. 1984; 200 g $C \cdot m^{-2} \cdot yr^{-1}$ [gross] estimated by T. R. Fisher [pers. comm.] from Melack and Fisher [1983]) tend to be less, and therefore reinforce these conclusions.

Zooplankton does not, of course, have to depend on phytoplankton but also utilizes detritus and bacteria (Brandorff [1977] in Junk 1984a). High densities of zooplankton of 13–15 $g \cdot m^{-3}$ have been reported (Fisher 1979). However, Junk (1973, 1976) reported very high densities of up to 780 000$\cdot m^{-2}$ of invertebrates associated with macrophytes, many of which depend on detritus. Conversely, benthic invertebrates are very limited due to seasonally low dissolved oxygen over much of the substrate (Reiss 1976). In general, the várzea floodplain can be regarded as a heavily-respiring system (Wissmar et al. 1981; Melack and Fisher 1983), with most photosynthesized carbon passing through a detritus phase. Fish biomass was strongly associated with emergent macrophyte stands in the várzea, and many species are detritivorous (Bayley 1983). However, a preliminary analysis of $\delta^{13}C$ from five adult detritivorous characins and various carbon sources was consistent with the hypothesis that they fed on carbon originating in phytoplankton (Araujo-Lima et al. 1986).

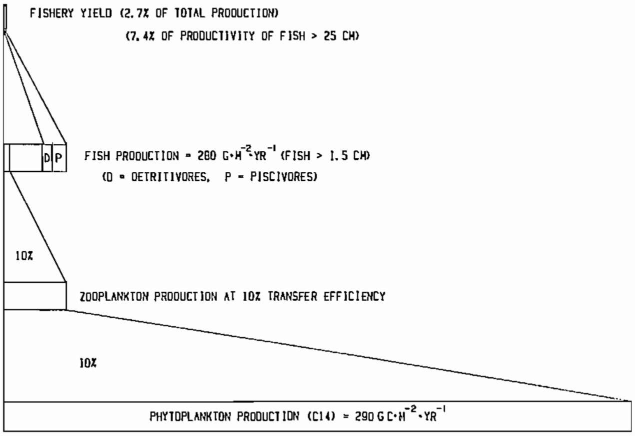

FIG. 4. Comparison of fish yield, "fish" production (including 1 % *Macrobrachium*), phytoplankton production (Schmidt 1973b) and hypothetical production of zooplankton dependent on phytoplankton in 5 330 km^2 of várzea floodplain on the lower R. Solimões.

Estimates of five major sources of photosynthesized or transported carbon with fish production are compared (Table 1) in the study area. These sources, except for phytoplankton mentioned previously, are discussed below.

The photosynthesized carbon from within the várzea floodplain was dominated by macrophytes and the seasonally flooded forest (Table 1). The macrophyte estimates of Junk (1985) and Junk and Howard-Williams (1984) (Table 1) are the highest reported (cf. Brinson et al. 1981) but most estimates are from cooler or more nutrient-limiting environments, and usually fail to account for all components of productivity. An estimate including both emergent-aquatic and terrestrial macrophytes within the várzea was made (Table 1) because both inputs are likely to be important in fish production (Junk 1980; Bayley 1980).

There are no rooted, submerged macrophytes and few floating, submerged macrophytes (e.g. *Utricularia*) in the várzea because of adverse light conditions (Junk 1984a). Similarly, epiphytic algae appears to be limited (Junk 1973), but as várzea water clears periphyton aufwuchs communities develop locally, even on submerged branches in the nutrient-poor igapó forest (M. Goulding, pers. comm.), and filamentous algae feature in the diet of some fish species (Santos 1981).

Using oxygen methods, T. R. Fisher (pers. comm.) estimated a periphyton gross production of 0.77 g $C \cdot m^{-2} \cdot d^{-1}$

TABLE 1. Primary and fish production estimates in the central Amazon vãrzea floodplain. Region includes 187 km of the R. Solimões between the R. Negro and R. Purus confluences and a maximum flooded area[a] of 5 330 km^2

Carbon source	Carbon production		
	as tonnes of carbon per km^2 per yr.	as tonnes of carbon per yr	as % of total primary production
Phytoplankton[b]	290	191 000	5.4
Periphyton[c]	280	52 000	1.5
Aquatic macrophytes[d]	2 000	818 000	22.9
Terrestrial macrophytes[d]	2 000	1 638 000	45.9
Flooded, várzea forest (litter only)[e]	500	870 000	24.4
Total annual primary production		3 569 000	100
Annual fish production[f]		36 600	1.03
Annual fishery yield [g]		960	0.027

[a] Areas (within quadrats 2–10, Fig. 3.) corresponding to respective carbon sources estimated using LANDSAT multispectral analysis (Bayley and Moreira 1980), LANDSAT near-infrared and side-scanning radar (RADAMBRASIL 1976) images, combined with ground truth observations (Bayley 1983). 22 % of the total flooded area consisted of poorly drained, marginal swamps or wet grassland, and was discounted. The remaining, "active" floodplain, consisted of the "white water" R. Solimões channel (17 %), flooded forest (42 %), and permanent, "black" water (11 %). Other, seasonally variable components are given below.

[b] Using seasonally weighted C14 estimates of Schmidt (1973b) (290 g C•m^{-2}•yr^{-1}) and annual mean area of "decanted" and "mixed" water of 660 km^2 (Bayley and Moreira 1980); the other water types, "black" and "white" have neglibible net productivity.

[c] Using preliminary estimate of 0.77 g C•m^{-2}•d^{-1} gross primary production from T. R. Fisher (see text). Extrapolated on the basis of seasonal aquatic macrophyte coverage: a linear increase of aquatic macrophyte area from 0 to 409 km^2 during 7 months from December through June and a constant maximum value during July and August. Does not include periphyton using other substrates.

[d] Using an average, annual net production during dry period of 40 t•ha^{-1} dry weight (Junk 1985), (also Junk and Howard-Williams [1984] estimated 39 t•ha^{-1} for the common semi-aquatic grass *Paspalum fasciculatum* during its terrestrial phase). The area within the 'active' floodplain which is seasonally covered with terrestrial or aquatic macrophytes totalled 1 228 km^2, in which aquatics reached a maximum of 409 km^2. Since the production estimate was based on an annual cycle from a fixed area, the total area was used to estimate production of all macrophytes, and the aquatic component was assumed to be proportional to the ratio of the areas (409/1 228 = about a third of the total). A carbon content of 50 % of dry weight was assumed.

[e] Using estimate of 10 t•ha^{-1}•yr^{-1} dry weight average litterfall from Adis and Klinge (1988, in Soares et al. 1986), and based on 1 740 km^2 of flooded forest. Carbon content of 50 % of dry weight assumed.

[f] See text. *Macrabrachium* comprises 1 % of estimate. Data seasonally corrected for a "productive area" varing between 700 and 2 100 km^2 (Bayley 1984), which excluded "black" water areas, but included extrapolation to várzea forest which is influenced by white water.

[g] Commercial and local market/subsistance yield (Bayley 1981); carbon content of 10 % of fresh weight assumed.

(SE of .33, 10 samples) in Lago Calado within the study area. Measurements were taken between December and August during the rising and maximum water levels (Fig. 2). Outside this period semi-aquatic macrophyte beds, which form the major substrate for periphyton in areas influenced by white waters, are negligible. Based on seasonal changes in emergent macrophyte coverage, an annual gross periphyton production of 5.2 × 10^4 t was estimated (Table 1). This is based on preliminary data, and excludes periphyton using submerged wood, principally in the igapó forest. Production per unit area of substrate is lower in such habitats (T. R. Fisher, pers. comm., from unpublished data by L. F. Alves).

Adis et al. (1979) estimated 6.7 t•ha^{-1}•yr^{-1} dry weight of litterfall in the nutrient-poor igapó forest of the R. Negro. Flowing water forested wetlands in south temperate areas produce up to 6.2 t•ha^{-1}•yr^{-1} (Brinson et al. 1981). Nutrients are much more abundant in the várzea than in the igapó (Fittkau et al. 1975) and higher litterfall values would be expected. Recently, Adis and Klinge (in Soares et al. 1986) reported an average annual litter production of 10 t•ha^{-1} dry weight from várzea forest. This is within the range of four tropical riverine forests quoted in Brinson (in press) which produced an annual mean of 13 ±3 (SD) t•ha^{-1}. This may be an underestimate, because there could be a significant contribution of carbon from wood production. The higher minimum water levels since the mid 1960's near Manaus have resulted in considerable mortality of trees which have remained standing and must contribute carbon to the aquatic system in the long term.

The study area is dominated hydrologically by the R. Solimões main channel, and allochthonous contributions from inflowing streams are negligible. A maximum possible contribution of organic carbon to the floodplain is estimated, notwithstanding the probability that there is a net outflow during the annual cycle (A. H. Devol, pers. comm.), which would be a loss to the system in addition to carbon dioxide.

Organic carbon was estimated from R. Solimões concentrations between January and July at Anorí near the upstream end of the study area, and at Manacupuru near the center. POC data were obtained by combining the percentage of carbon in suspended sediments (Hedges et al. 1986: Table 3) with the corresponding fine and coarse suspended sediment concentrations of Richey et al. (1986: Table 3) producing a mean of 3.05 ±.84 (SD) mg•L^{-1} from 4 samples. DOC data from 10 samples (A. H. Devol, pers. comm.) averaged 3.93 ±.55 (SD) mg•L^{-1}. If the total organic carbon concentration of 6.98 mg•L^{-1} flooded the whole várzea (4 650 km^2) to a depth of 1 m and was not returned to the main channel, the net gain would be 3.25

× 10^4 t, which would only constitute 0.9% of the autochthonous primary production in the floodplain (Table 1). Moreover, the DOC fraction is mostly refractory (Ertel et al. 1986) as is most of the POC (Hedges et al. 1986).

The fish production estimate (Table 1) is one of the highest reported, but comparable estimates from other tropical floodplains are lacking. The estimate is only applied to a "productive area" within the study area (Bayley 1983, 1984) which excludes the smaller areas occupied by black waters, swamps, and the main river channels, which indicate much lower fish productivity (Fittkau et al. 1985; Junk et al. 1988). Therefore, by excluding low productivity areas and the productivity of fish under 15 mm, the fish production total (Table 1) is considered an underestimate when applied to the whole study area (Fig. 3).

Discussion

The relative contribution of each source to fish production may, of course, be very different from their relative productivities. However, these results suggest that the overall trophic roles of phytoplankton and periphyton are minor, and the qualitative observations of fish depending on higher plants mentioned previously appear to be very significant. However, the periphyton estimate is preliminary, and was only based on one major substrate (macrophytes). The total production and role of periphyton, in particular with respect to younger fish, needs to be investigated.

Eighteen percent of the várzea fish productivity (Bayley 1983; Fig. 4) and 34% of the fishery yield to Manaus (Petrere 1982) consisted of detritivores (Prochilodontidae, Curimatidae) which principally feed on fine detritus and associated bacteria and fungi. Araujo-Lima et al. (1986) claim that these families derive most of their carbon from phytoplankton-based food chains. They analysed $\delta^{13}C$ from five adult detritivorous characin species (excluding the very abundant *Semaprochilodus insignis*), 7 phytoplankton samples, and a variety of other carbon sources. Their hypothesis depends on the low values of $\delta^{13}C$ for phytoplankton, which contained up to 40% of unidentified POC, and the lack of other sources of equal or lower values.

It is indeed plausible that phytoplankton carbon may feature more in the diet of adults, since they migrate long distances in open waters but frequently pause to feed (A. Guedes dos Santos, pers. comm.). Most of the fish production of detritivorous characins in várzea habitats is accounted for by juveniles (Bayley 1983). Unless the various phytoplankton productivity estimates cited are all grossly underestimated, it is difficult for this source to account for the entire productivity of this group in addition to that of pelagic (e.g. *Colossoma macropomum*, Engraulidae, *Hypophthalmus* spp., *Anodus* spp.) and young stages of fish which are strongly associated with the plankton or zooplankton. Moreover, it has been estimated that about 20% of annual phytoplankton production was buried annually in a várzea lake (Devol et al. 1984). What is the fate of the enormous production of macrophytes which occurs in the presence of a significant proportion of the fish biomass? Are the plants or their detritus largely ignored by fish or their prey, and the carbon respired or buried?

I would regard 1.03% of the estimated total primary production being manifested as fish production (Table 1) as being quite efficient, considering the variety of avian and terrestrial consumers in the floodplain, and the fact that larger aquatic consumers in the main channel, such as piscivorous catfish and dolphins, could not be included. If the data had come from an "ideal" lake system with a simple phytoplankton–invertebrate–fish process, a fairly efficient system with 10% transfer efficiencies linking only three trophic levels could be inferred.

In contrast, the fishery yield was only 2.6% of fish production, which is considered low for various reasons. Most marketed fish exceed 25 cm in length, but the fishery yield was still only 7.4% of the production of fish exceeding this length. This can be partly attributed to underutilization of many species (Bayley 1981; Petrere 1982). However, if the utilization and fishing intensity could be substantially increased to produce the empirically derived maximum yield of about 120 kg per hectare of maximum flooded area (Bayley 1988), this would only be 17% of fish production, or 48% of production of fish >25 cm long.

A large amount of "internal consumption" of fish productivity may be responsible for the small proportion of fish productivity manifested as yield. Large quantities of piscivores (Bayley 1983; Bayley and Petrere 1989) not only populate floodplain habitats, but white water rivers contain many dolphins and large catfish which consume numerous migratory characoid species such as the large *Colossoma macropomum* (M. Goulding, pers. comm.). A significant additional trophic level of piscivores would markedly reduce the amount of fish production manifested as yield.

This rudimentary consideration of carbon flow suggests that major vegetation types in the várzea floodplain are important for the maintenance of fish productivity. In turn, they are dependent on the maintenance of the hydrological cycle (Fittkau et al. 1975; Junk 1980). However, this preliminary analysis involves the extrapolation of limited primary production estimates. The complexity of the system indicates that even the most marginally realistic production models will be difficult to test empirically. The small amount of photosynthesized carbon appearing in the fish yield (Table 1) is very sensitive to the fishery and fish community dynamics which may mask temporal or regional differences in primary productivity. It is unlikely that more detailed knowledge of the primary and secondary processes leading to fish production will improve our ability to predict fish yields.

However, these results support the comparative fishery analysis in Bayley and Petrere (1989) that potential for fisheries expansion exists in most parts of the basin provided that environmental factors such as hydrology and vegetation cover do not deteriorate. Regular flood pulses are vital to the productivity of such systems (Junk et al. 1989). In the light of deforestation and hydroelectric dam construction in progress, the dependency of fish production on a variety a carbon sources outlined in this paper is a vital consideration. There is no guarantee that a significant change in hydrology or vegetation would allow an expansion of, or even a maintenance of the present yields. However, it is virtually certain that the species composition of the yield would change.

Research Needs

Although I question the utility of improved quantitative tropho-dynamic data for the purposes of predicting fishery yields, efforts to understand the important linkages in the system are important for the science in general and to predict the consequences of environmental alteration in the Amazon in particular.

A better understanding of tropho-dynamic relationships is possible using stable isotope ratios combined with traditional diet analysis. The pioneering work of Hedges et al. (1986) and Araujo-Lima et al. (1986) needs to be expanded with respect to isotope ratios of other elements. Also, compositions of sources and intermediate links indicated by diet analyses, and of different life stages of fish are needed on a habitat-specific basis.

Qualitative linkages indicated by isotope ratio and diet studies need to be put in a quantitative context on an appropriate scale. The latter is dictated by the most mobile elements: fish. This means that improved primary production estimates which take into account spatial variation and habitat differences within the study area, in particular for periphyton, are necessary on a seasonal basis. Improved area-by-season measurements of principal productive zones are needed to scale these measurements. Attempts to estimate fish production in black waters and inundated forest are important, and the complex interactions among fish and between man and fish which account for such a tenuous link between fish production and fish yield need to be better understood.

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References

ADIS, J., K. FURCH, AND U. IRMLER. 1979. Litter production of a central Amazonian black water inundation forest. Trop. Ecol. 20: 236–245.

ADIS, J., AND H. KLINGE. 1988. Streufall im Várzea-Wald der Marchantaria Indel. Amazoniana. (in press)

ARAUJO-LIMA, C. A. R. M., B. R. FORSBERG, V. REYNALDO, AND L. MARTINELLI. 1986. Energy sources for detritivorous fishes in the Amazon. Science 234: 1256–1258.

ALMEIDA, R. G. 1980. Aspectos taxonômicos e hábitos alimentares de três espécies de *Triportheus* (Pisces: Characoidei, Characidae), do lago do Castanho, Amazonas. M. Sc. thesis, INPA, Manaus, Brazil. 104 p.

BAYLEY, P. B. 1980. The limits of limnological theory and approaches as applied to river-floodplain systems and their fish production, p. 739–746. *In* J. I. Furtado [ed.] Tropical ecology and development. Proceedings of the Vth International Symposium of Tropical Ecology. International Society of Tropical Ecology, Kuala Lumpur.

1981. Fish yield from the Amazon in Brazil: comparisons with African river yields and management possibilities. Trans. Am. Fish. Soc. 110: 351–359.

1983. Central Amazon fish populations: biomass, production and some dynamic characteristics. Ph.D. thesis, Dalhousie University, Halifax, Nova Scotia, Canada. 330 p.

1984. Aquatic productivity in the central Amazon várzea in the context of the fishery yield. 17 p. *In* Primer Simpósio do Trópico Umido, 12–17 November 1984. Belém, Brazil.

1988. Accounting for effort when comparing tropical fisheries in lakes, river-floodplains and lagoons. Limnol. Oceanogr. (In press) 33: 963–972.

BAYLEY, P. B., AND J. C. MOREIRA. 1980. Preliminary interpretations of aquatic resources in the Central Amazon Basin using LANDSAT multispectral imagery, p. 861–868. *In* J. I. Furtado [ed.] Tropical ecology and development. Proceedings of the Vth International Symposium of Tropical Ecology. International Society of Tropical Ecology, Kuala Lumpur.

BAYLEY, P. B., AND M. PETRERE JR. 1989. Amazon fisheries: assessment methods, current status, and management options, p. 385–398. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

BRINKMAN, W. L., AND V. M. SANTOS. 1973. Heavy fish kill in unpolluted floodplain lakes of Central Amazonia, Brazil. Biol. Conserv. 5: 147–149.

BRINSON, M. N. 1988. Riverine forests. *In* A. E. Lugo, M. N. Brinson, and S. Brown [ed.] Forested Wetlands (Ecosystems of the World, vol. 15). Elsevier, Netherlands. (In press)

BRINSON, M. N., A. E. LUGO, AND S. BROWN. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. Ann. Rev. Ecol. Syst. 12: 123–162.

CARVALHO, M. L. 1981. Alimentação do tambaqui jovem (*Colossoma macropomum*) e sua relação com a comunidade zooplanctônica do lago Grande-Manaquiri, Solimões-AM. M.Sc. thesis, INPA, Manaus, Brazil.

DEVOL. A. H., T. M. ZARET, AND B. R. FORSBERG. 1984. Sedimentary organic matter diagenesis and its relation to the carbon budget of tropical Amazon floodplain lakes. Verh. Internat. Verein. Limnol. 22: 1299–1304.

ERTEL, J. R, J. I. HEDGES, A. H. DEVOL, AND J. E. RICHEY. 1986. Dissolved humic substances of the Amazon River system. Limnol. Oceanogr. 31: 739–754.

FISHER, T. R. 1979. Plankton and primary production in aquatic systems of the central Amazon Basin. Comp. Biochem. Physiol. 62A: 31–38.

FITTKAU, E. J., U. LEMLER, W. S. JUNK, F. REISS, AND G. W. SCHMIDT. 1975. Productivity biomass, and population dynamics in Amazonian water bodies, p. 289–311. *In* Z. B. Golley and B. Medina [ed.] Tropical ecological systems, Springer-Verlag, New York, NY.

GENTRY, A. H., AND LÓPEZ-PARODI. 1980. Deforestation and increased flooding of the upper Amazon. Science 210: 1354–1356.

GIBBS, R. J. 1967. The geochemistry of the Amazon river system: Part 1. The factors that control the salinity and the composition and concentration of the suspended solids. Geol. Soc. Am. Bull. 78: 1203–1232.

1970. Circulation in the Amazon River estuary and adjacent Atlantic Ocean. J. Mar. res. 28: 113–123.

GOULDING, M. 1980. The fishes and the forest. California University Press, CA.

HANEK, G. [ED.]. 1982. La pesqueria en la amazonia peruana: presente y futuro. Documento Técnico de Pesca, FAO, Rome.

HEDGES, J. I., W. A. CLARK, P. D. QUAY, J. E. RICHEY, A. H. DEVOL, AND U. M. SANTOS. 1986. Compositions and fluxes of particulate organic material in the Amazon river. Limnol. Oceanogr. 31: 717–738.

IRION, G. 1984. Sedimentation and sediments of Amazonian rivers and evolution of the Amazonian landscape since Pliocene times, p. 201–214. *In* H. Sioli [ed.] The Amazon (Monographiae biologicae, Vol. 56). Dr. W. Junk, Dordrecht, Netherlands.

JANZEN, D. H. 1974. Tropical black water rivers, animals and mast fruiting by the Dipterocarpaceae. Biotropica 6: 69–103.

Junk, W. J. 1973. Investigations on the ecology and production biology of the floating meadows (Paspalo-Echinochloetum) on the Middle Amazon, Part 2: the aquatic fauna in the root zone of floating vegetation. Amazoniana 4: 9–102.

1976. Faunal ecological studies in inundated areas and the definition of habitats and ecological niches. Anim. Res. Dev. 4: 47–54.

1980. Areas inundáveis — Um desafio para Limnologia. Acta Amazonica 10: 775–795.

1983. Ecology of swamps on the middle Amazon, p. 269–294. *In* A. J. P. Gore [ed.] Mires: swamp, bog, fen and moor, B. Regional studies.

1984a. Ecology of the várzea, floodplain of Amazonian whitewater rivers, p. 215–244. *In* H. Sioli [ed.] The Amazon (Monographiae biologicae, Vol 56). Dr W. Junk, Dordrecht, Netherlands.

1984b. Ecology, fisheries and fish culture in Amazonia, p. 443–476. *In* H. Sioli [ed.] The Amazon (Monographiae biologicae, Vol. 56). Dr. W. Junk, Dordrecht, Netherlands.

1985. The Amazon floodplain — a sink or source for organic carbon?. Mitt. Geol. Paläontol. Inst. Univ. Hamburg, SCOPE/UNEP Sonderbd. 58: 267–283.

Junk, W. J., and C. Howard-Williams. 1984. Ecology of aquatic macrophytes in Amazonia, p. 269–294. *In* H. Sioli [ed.] The Amazon (Monographiae biologicae, Vol 56). Dr W. Junk, Dordrecht, Netherlands.

Junk, W. J., and J. A. S. deMello. 1987. Impactos ecológicos das represas hidroelétricas na bacia amazônica brasileira, p. 367–385. *In* G. Kohlhepp and A. Schrader [ed.] Homen e natureza na Amazonia, Tübinger Geogr. Studien 95.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river–floodplain systems, p. 110–127. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Klammer, G. 1984. The relief of the extra-Andean Amazon basin, p. 47–84. *In* H. Sioli [ed.] The Amazon (Monographiae biologicae, Vol 56). Dr. W. Junk, Dordrecht, Netherlands.

Meade, R. H., C. F. Nordin, Jr., W. F. Curtis, F. M. C. Rodriguez, R. M. Vale, and J. M. Edmund. 1979. Transporte de sedimentos no Rio Amazonas. Acta Amazonica 9: 543–547.

Melack, J. M., and T. R. Fisher. 1983. Diel oxygen variations and their ecological implications in Amazon floodplain lakes. Arch. Hydrobiol. 98: 422–442.

Milliman, J. D., and R. H. Meade. 1983. World-wide delivery of river sediments to the oceans. J. Geol. 91: 1–21.

Nimer, E. 1977. Clima, p. 39–58. *In* Geografia do Brasil: Região Norte. Instituto Brasileiro de Geografia e Estatistica (IBGE), Rio de Janeiro, Brazil.

Nordin, C. F., and R. H. Meade. 1982. Deforestation and increased flooding of the upper Amazon. Science 215: 426–427.

Paixão, I. M. P. 1980. Estudo da alimentacão e reproducão de *Mylossoma duriventris* (Pisces, Characoidei), do Lago Janauacá, Am., Brasil. M.Sc. thesis, INPA, Manaus, Brazil. 127 p.

Petrere, M., Jr. 1982. Ecology of the fisheries in the River Amazon and its tributaries in the Amazonas State (Brazil). Ph.d. thesis, University of East Anglia, UK. 96 p.

Radambrasil. 1976 Projecto Radambrasil: Levantamento de recursos naturais (15 volumes). Ministerio das Minas e Energia, Rio de Janeiro, Brazil.

Reiss, F. 1976. Charakterisierung zentral amazonischer Seen aufgrund ihrer Makrobenthosfauna. Amazoniana 6: 123–134.

Richey, J. E., R. H. Meade, E. Salati, A. H. Devol, C. F. Nordin, and U. M. Santos. 1986. Water discharge and suspended sediment concentrations in the Amazon river. Water Resources Research 22: 756–764.

Salati, E., and P. B. Vose. 1984. Amazon basin: a system in equilibrium. Science 225: 129–138.

Santos, G. M. 1981. Estudos de alimentação e hábitos alimentares de *Schizodon fasciatus* Agassiz, 1829, *Rhytiodus microlepis* Kner, 1859 e *Rhytiodus argenteofuscus* Kner, 1859, do lago Janauacá-AM. (Osteichthyes, Characoidei, Anostomidae). Acta Amazônica 11: 267–283.

Schmidt, G. W. 1973a. Primary production of phytoplankton in the three types of Amazonian waters. II. The limnology of a tropical flood-plain lake in Central Amazonia (Lago do Castanho). Amazoniana 4: 139–203.

1973b. Primary production of phytoplankton in the three types of Amazonian waters. III. Primary productivity of phytoplankton in a tropical flood-plain lake of Central Amazonia, Lago do Castanho. Amazonas, Brazil. Amazoniana 4: 379–404.

Sioli, H. 1964. General features of the limnology of Amazônia. Verh. Internat. Verein. Limnol. 15: 1053–1058.

1966. General features of the delta of the Amazon, p. 381–390. *In* Scientific problems of the humid zone deltas and their implications. Proceedings, Dacca Symposium, UNESCO.

1973. Recent human activities in the Brazilian Amazon region and their ecological effects, p. 321–334. *In* B. J. Meggers, E. S. Ayensu, and W. D. Duckworth [ed.] Tropical forest ecosystems in Africa and South America: a Comparative Review. Smithsonian Institution Press, Washington, USA.

1984. The Amazon and its main affluents: hydrography, morphology of the river courses, and river types, p. 127–166. *In* H. Sioli [ed.] The Amazon (Monographiae biologicae, Vol. 56). Dr. W. Junk, Dordrecht, Netherlands.

Soares, M. G. M., R. G. Almeida, and W. J. Junk. 1986. The trophic status of the fish fauna in Lago Camaleão, a macrophyte dominated floodplain lake in the middle Amazon. Amazoniana 9: 511–526.

Stallard, R. F.. 1980. Major element geochemistry of the Amazon River system. Ph.D. thesis, M.I.T.-W.H.O.I. Joint Program in Oceanography, Cambridge, MA.

Stallard, R. F. and J. M. Edmond. 1981. Geochemistry of the Amazon 1. Precipitation chemistry and the marine contribution to the dissolved load at the time of peak discharge. J. Geophys. Res. 86(C10): 9844–9858.

Vieira, I. 1982. Aspectos sinecológicos da ictiofauna de Curuá-Una, represa hidroelétrica da Amazônia Brasileira. Thesis, Universidade Federal de Juiz de Fora, Minas Gerais, Brazil. 107 p.

Wallace, A. R. 1853. A narrative of travels on the Amazon and Rio Negro. 541 p.

Welcomme, R. L. 1979. Fisheries ecology of floodplain rivers. Longman, London, 317 p.

Welcomme, R. L., and D. Hagborg. 1977. Towards a model of floodplain fish populations and its fishery. Environ. Biol. Fish. 2: 7–24.

Wissmar, R. C., J. E. Richey, R. F. Stallard, and J. M. Edmond. 1981. Plankton metabolism and carbon prodcesses in the Amazon river, its tributaries, and floodplain waters, Peru–Brazil, May–June 1977. Ecology 62: 1622–1633.

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Some Ecological Aspects and Present State of the Fishery of the Magdalena River Basin, Columbia, South America

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Abstract

VALDERRAMA, M., AND M. ZÁRATE. 1989. Some ecological aspects and present state of the fishery of the Magdalena River basin, Columbia, South America, p. 409–421. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The Magdalena River basin (256 622 km^2) contains a tropical river system with periodically inundated plains; the Magdalena (1538 km) is its principal river and has, together with its most important tributaries, a maximum floodplain of 20 024 km^2 and a permanent one of 3260 km^2. Seventy-seven percent of Colombia's 26 million population live in the basin, and the country's main industrial centers are also located there. Pollution, deforestation, modification of the river for navigation, land management for agriculture and cattle raising on the floodplain, and the damming of the rivers are today's chief ecological impacts. The basin contributes 85 % of Colombia's production of freshwater fish, totalling a mean of 49 378 t•yr^{-1}. The physical environment is dominated by a flood regime whose fluctuations are the main regulator of the limnological processes. Many fish species migrate into and out of the rivers and floodplain lakes and are the mainstay of a very important seasonal fishery during low waters. There are 166 fish species, of which 26 are economically significant. The mean fish biomass of 68.2 kg•ha^{-1} in the floodplain is low, possibly due to the significant movement of fish out of the floodplain toward the rivers. The Magdalena River basin's yield was estimated as 40 kg•ha^{-1}•yr^{-1} for 1977, based on the maximum flood area. Since 1981 a marked decrease in the total catch has been observed. The principal management strategies are directed towards strengthening the legislation for the prevention of environmental degradation. The aim for fisheries is to guarantee a sustained yield. Programs, in an infrastructure of 13 research and production centers, are being promoted to increase yields by aquaculture. As a socioeconomic alternative, fishing communities are being organized to receive not only integrated development programs but also aquaculture production as well.

Résumé

VALDERRAMA, M., AND M. ZÁRATE. 1989. Some ecological aspects and present state of the fishery of the Magdalena River basin, Columbia, South America, p. 409–421. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Le bassin de la rivière Magdalena (256 622 km^2) contient un réseau de rivière tropicales avec des plaines périodiquement inondées; la Magdalena (1 538 km) constitue le principal cours d'eau du réseau et, avec ses principaux tributaires, compte au maximum 20 024 km^2 de plaines d'inondation et 3 260 km^2 de plaines d'inondation en permanence. Soixante-dix-sept pour cent de la population de la Colombie, qui compte 26 millions d'habitants, vit dans ce bassin; les principaux centres industriels du pays y sont également réunis. La pollution, le déboisement, la modification de la rivière pour la navigation, la gestion des sols pour fins agricoles et l'élevage du bétail dans la plaine d'inondation ainsi que les ouvrages jetés sur les rivières, constituent les principales sources de répercussions écologiques actuelles. Quatre-vingt-cinq pour cent de la production colombienne de poissons d'eau douce, 49 378 t•an^{-1}, provient de ce bassin. L'environnement physique est dominé par un régime d'écoulement dont les fluctuations constituent le principal agent régulateur des processus limnologiques. Beaucoup d'espèces descendent les cours d'eau ou les remontent jusqu'aux lacs de la plaine d'inondation; ils constituent la base d'une pêcherie saisonnière très importante en période d'étiage. On a dénombré 116 espèces dont 26 ont une importance économique. La biomasse moyenne de poissons dans la plaine d'inondation, qui se chiffre à 68,2 kg•ha^{-1}, est faible, peut-être à cause de l'important déplacement des poissons qui quittent la plaine d'inondation pour se rendre dans les rivières. Le rendement dans le bassin de la rivière Magdalena a été évalué à 40 kg•ha^{-1}•an^{-1} en 1977, en prenant la superficie maximum d'inondation comme base de calcul. Depuis 1981, on observe une nette régression de la prise totale. Les principales stratégies de gestion visent à renforcer les mesures législatives adoptées pour contrer la dégradation du milieu. Avec les pêches, l'objectif est de garantir l'obtention d'un rendement soutenu. Des programmes appliqués par l'intermédiaire de 13 centres de production et de recherche sont proposés pour augmenter les rendements par l'aquaculture. Comme solution de rechange socio-économique, les communautés qui vivent de pêche sont organisées de façon à être bénéficiaires de programmes de développement intégrés, mais aussi de production par l'aquaculture.

Introduction

The objective of this paper is to provide information on the ecology of the Magdalena River and floodplain system and to describe the present state of the fishery. The paper discusses various aspects of fish populations, limnology, stock assessment, catch assessment as well as fishery management strategies that have been introduced.

Freshwater fisheries in Colombia generated an annual catch of 49 378 $t \cdot yr^{-1}$ during 1983–84 (Instituto Nacional de los Recursos Naturales Renovables y del Ambiente 1985), representing 72 % of the total national fish production for commercial consumption including yield from marine waters. The Magdalena River basin contributed 85 % of the freshwater fish production, which demonstrates the great significance of this basin for Colombia.

Approximately 77 % of the Colombia population, amounting to 26 million, lives in the Magdalena River basin (Uries 1976). This concentration of people, coupled with significant industrial, agricultural, and cattle raising activities within the basin, have generated intense pressure on land and water resources.

Description and Utilization of the Basin

The Magdalena River basin is formed by the eastern, central, and western ranges of the Andes mountains, and follows an approximately South–North direction, between 2°N–11°N and 73°W–77°W (Fig. 1). The basin covers an area of 256 622 km^2 and drains into the Caribbean Sea. The upper and middle zones are contained within two long, narrow valleys which join to form a vast region of savanna that ends at the Caribbean coastline. The region is tropical, but temperatures vary according to altitude. There are two rainy seasons each year, with most of the precipitation durint May–June and October–November.

The principal river of the basin is the Magdalena which has a length of 1538 km and an average annual discharge of 6800 $m^3 \cdot s^{-1}$. The Cauca River (1350 km) is its main tributary, joining the Magdalena in the central floodplain area, as does the San Jorge River (368 km). In the middle and lower part of the basin these rivers form a vast floodplain of shallow, polymictic lakes, known as ciénagas. Each year, 2 million ha of the floodplain may be inundated during short periods of 1 month, 1.6 million ha during a 1–3 month period, 1.3 million ha during 3–6 months, and 730 000 ha during 6–12 month periods (Pardo 1976). The area of permanent floodplain lakes is 326 000 ha with sizes of individual waterbodies ranging from 1 to 11 000 ha in area and 1 to 6 m in depth (Kapetsky et al. 1977a).

The floodplain lakes are natural reservoirs and greatly influence the fluviometric regime of the rivers. During flood peak, the lakes receive considerable amounts of water, which flow back gradually toward the rivers when their levels recede, thus regulating the fluctuations of the water level. For example, in the Magdalena River the ratio between low and high waters at the point where the floodplain starts is 1:10.8, while in the lower basin it is only 1:3.4. (Julius Berger Konsortium 1926).

The Magdalena River is divided into three sections: from its source to the city of Neiva (221 km), from Neiva to Honda (370 km) and from Honda to its mouth (947 km). From Neiva to just before Honda the slope is 2.6 to 0.3 %; near Honda, the river is a series of rapids, of which the so-called "Salto de Honda" features a slope of 5 %; downriver from Honda, and almost to Barrancabermeja, the slope ranges from 1.5 % to 0.32 % and from there to the mouth the slope is very shallow, ranging between 0.39 and 0.04 % (Kaufmann and Hevert 1973). The commercial fisheries are the most highly developed in this last section, while in the second section, Neiva to Honda, fishing is for subsistence purposes and, in general, minimal.

Depending on annual precipitation, water levels vary from a monthly low average of 2.6 m during March to a monthly high average of 6.7 m during December (Kaufmann and Hevert 1973). The four fishing seasons in the basin are closely related to water levels (Fig. 1). Bazigos et al. (1975) divided the hydrological year into four seasons: low waters (90 d duration), rising waters (31 d), high waters (153 d), and falling waters (90 d). Each of these periods depends on specific annual hydrological cycles sometimes significantly varying conditions.

Cattle and agriculture are the main activities within the river basin involving 70 % of its total area. In the alluvial plains, cattle raising is particularly significant (59 %), whereas agriculture is somewhat limited (34 %). Cattle rearing is of the scattered type with some 1.03–0.82 $heads \cdot ha^{-1}$ (Instituto Nacional de los Recursos Naturales Renovables y del Ambiente INDERENA 1981). The chief impacts of these two activities in the basin are deforestation and overgrazing which, together with other farming methods, have led to moderate to high intensity erosion factors, with sediment transport in the lower part of the Magdalena River being 26 million $m^3 \cdot yr^{-1}$ (Comisión de Pesca Continental para América Latina 1984). There are no data available for levels of agro-industrial chemicals in inland waters or in fish, but we suspect that they may be disturbingly high, because Colombia trades 21 000 $kg \cdot yr^{-1}$ and 18.4 million $L \cdot yr^{-1}$ of commercial pesticides (Comisión de Pesca Continental para América Latina 1984) and the control of applications is minimal. There is also no information as to the area of the floodplain that has been drained and lost to the fishery for agricultural and cattle raising purposes. This practice is not yet widespread, but should there be any trend to increase the area of reclaimed land, serious ecological effects on the fishery resources can be anticipated. Moves in this direction in the form of a program to extend the irrigated area in the lower part of the basin to 490 000 ha (presently 3900 ha) is under way. This includes the development of prefeasibility programs for flood control and land recovery in the floodplain (Mejía, Millán y Perry Ltda 1983), which will probably lead

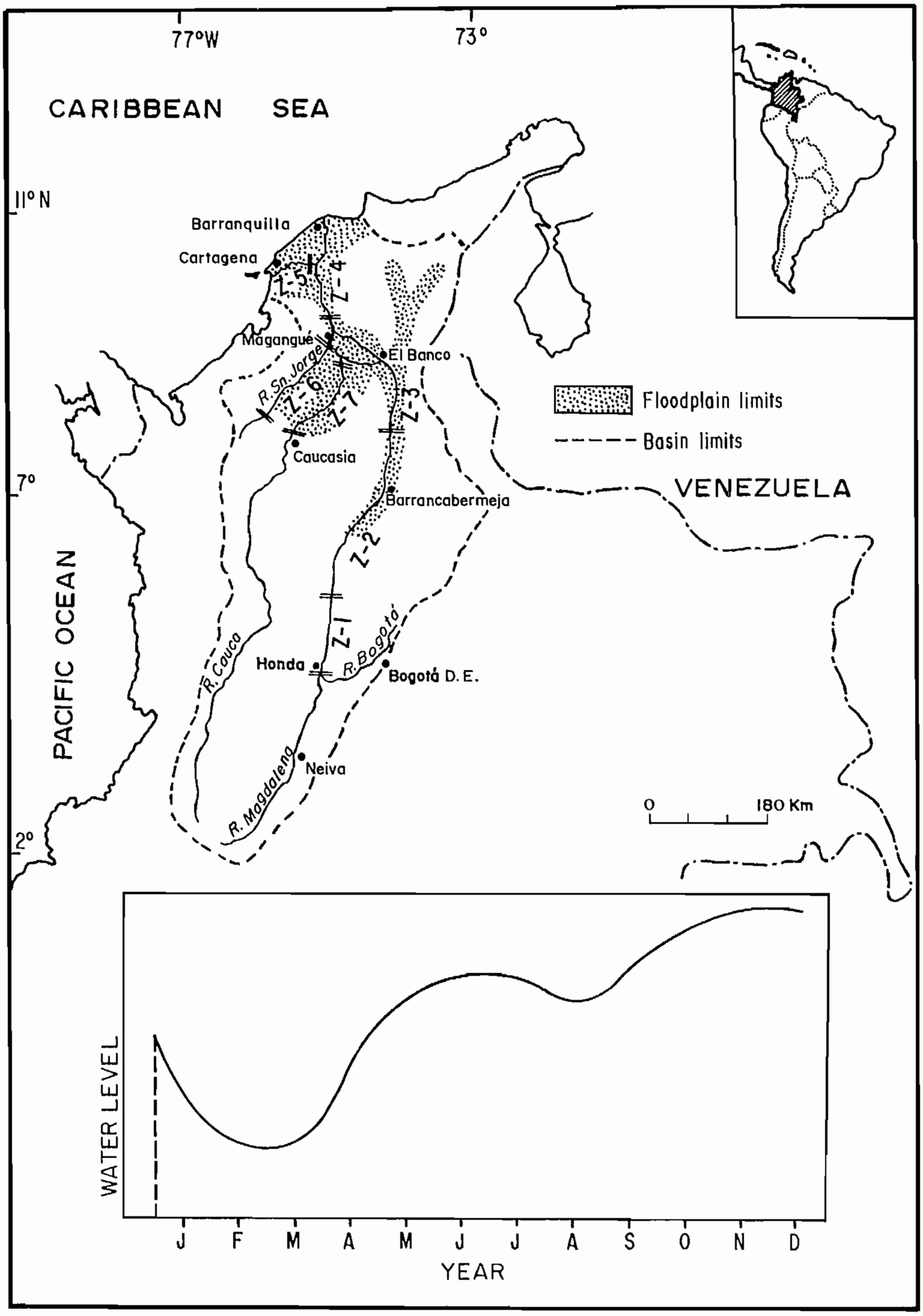

FIG. 1. Magdalena River basin with fishery zones, floodplain limits, and average water level variations.

to an alteration in the floodplain's hydrological regime, threatening fishery activities and yields.

The river is navigable for 1200 km upstream, which is why river transport has acquired special significance in the lower zones, where road systems are scarce. Thus, the rivers and floodplain are vitally important for local transportation. Currently, sedimentation of the chief navigation channels has greatly reduced the mean draught of commercial vessels (Instituto Nacional de los Recursos Naturales Renovables y del Ambiente 1984). One of the greatest problems at present is the reconditioning of the Canal del Dique, an artificial 118 km-long channel (See Fig. 1), for navigation purposes, which has led to impoundment and/or alterations in the hydrologic regime of the floodplain, variously affecting the 11 000 ha of floodplain lakes connected to the channel.

Cities are concentrated in the middle and high valleys of the Andean zone; Bogotá has over 4 million inhabitants and three other cities three have nearly 1.5 million, of which only one is located in the lower part of the basin on the banks of the Magdalena River: Barranguilla. The population along the river in 1981 was 2.7 million, and the basin total population in 1984 was 20 million (INDERENA 1984). These four urban centres lack water treatment systems. Industrial wastes from these four cities have caused a BOD = 356 260 kg•d^{-1} and a BOD from household waste of 276 310 t•yr^{-1} (Com. Pes. Cont. Amer. Lat. 1984). Mikkola (1976) stated that the quality of the Magdalena River water has decreased by 100 % for some parameters in the confluence with the Bogota River, which receives Bogota's sewage.

Major hydroelectric projects have flooded an area of 47 243 ha (Valderrama 1985). Damming has occurred on minor tributaries; since 1985 a dam (Salvajina, 2 031 ha) has impounded the Cauca's main channel at approximately 120 km from its source, and another is under construction (Betania, 7200 ha) which will dam the Magdalena River 260 km from its source. Some estimates predict that the present dams on the upper Magdalena River will not affect the hydrological regime in its middle and lower parts (Univers. Nac. 1985), but studies determining eventual impacts on fisheries are still in early stages.

Fish Communities

The basin belongs to the Magdalenian icthyofaunistic region of South America (Lowe-McConnell 1975). Dahl (1971) reported 166 fish species in the basin; 64 characoids, 7 gymnotoids, 64 siluroids of which 13 are pimelodids and 21 loricariids, 4 cichlids, 7 cyprinodonts, the remaining of which are other secondary fishes and of marine origin. The diversity is high, considering the basin's area (Miles 1971).

More than 42 species of two distinct groups are found in the floodplain (Table 1). In the first group are those species which migrate into and out of rivers and floodplain lakes, avoiding the harsh deoxygenation conditions during high temperature and low water seasons. In the second group are species which move within the floodplain, and which show great resistance to extreme conditions.

Most species reproduce when water levels are low or rising, although another reproduction season apparently takes place in October, at the beginning of the second period of rising waters (Fig. 2). The median lengths at gonadal maturity for 15 species of commercial significance are given in Table 2.

Spawning migrations in rivers are the most important phenomena in the basin: "subiendas" are when fish migrate upstream during low-water periods, and "bajanzas" are when species return to growing and feeding sites in the floodplain. Fishes start migrations in schools. The first species to migrate are smaller characids (*Triportheus magdalenae, Astyanax* spp.), followed by bigger characids (*Prochilodus reticulatus magdalenae, Brycon moorei, Salminus affinis*), and finally pimelodids (*Pseudoplatystoma fasciatum, Pimelodus* spp., *Sorubim lima*) (Hurtado 1972). The behaviour of *P. reticulatus magdalenae*, when the water level begins to fall, is to leave the floodplain lakes, form schools and then move upstream and enter the upper tributaries (Dahl et al. 1963).

When the rains begin, the "bajanza" occurs, the period for reproduction, with the larvae moving down the rivers near the banks. Hurtado (1972) demonstrated this behaviour pattern for *P. reticulatus* and likewise determined that *Pimelodus clarias* and *P. fasciatum* spawn in the main river channels. Larvae are carried by river currents, which concurs with Bayley (1973) who identified the early migration phase of *Prochilodus platensis* as being a drift.

Limnology

The main rivers in the Magdalena basin are generally very turbid, with alkaline pH, and relatively high conductivity. Table 3 shows limnological measurements carried out in the Magdalena, Cauca and San Jorge rivers by means of a Hach-DR Kit.

Three types of habitat occur in the floodplain lakes: open water, bays or coves with surface areas of less than 25 ha, and shores usually covered by vegetation. There is no marked difference between habitats, although greater amounts of benthos and phytoplankton occur in bays than in open waters (Table 4). Coastal vegetation is richer along the bays, providing feeding sources for fish.

During low water, floodplain lakes become more productive because of higher temperatures, concentration of nutrients, and greater solar radiation. When the rains start again flooding causes greater turbidity and a reduction in plankton. However, macrophytes and their associated fauna rapidly increase production during the course of the first season (Mikkola y Arias 1975).

Fish production in the river floodplain system is related to quantities of detritus washed into floodplain lakes from the river channel and to terrestial inputs when floodwaters spread over the floodplain. Therefore, high rainfall and high water levels would also affect fish production, especially in fishes adapted to detritus feeding.

Standing Stock

Kapetsky et al. (1977a) carried out a stock assessment program; 29 estimates were performed between 1975 and 1976, using the method of fencing 0.25 ha areas with a blocking net 4.5 m deep and of 2.5 cm stretched mesh. The estimates were made at times of low water, mid-rising, mid-falling and at high flood. To collect fish, rotenone was introduced in the enclosed area at concentrations between 0.5 and 2.0 mg•L^{-1}. After recovering the affected fishes, three fleets of 2.5–15.2 cm stretched mesh, multimesh monofilament gillnet were set inside the enclosure for 24 h to catch fish unaffected by the rotenone.

The most frequently occurring fish in the floodplain was the small characid *Roeboides dayi*, found in 97 % of the sampling sites (Fig. 3). Only 12 of the 42 fish species present in floodplain lakes were collected in half of the sampling sites, suggesting that the fish are not evenly distributed within the lakes, that 28 % are predators, and many of the important fish species feed on detritus.

Table 1 indicates, for two different types of habitat, the biomass estimated for the 14 most abundant species. The mean biomass found when the 29 samples were combined was 68.2 kg•ha^{-1} (± 35 % with 95 % confidence), with estimates ranging from 0.2 to 251.4 kg•ha^{-1}. Biomass estimates for both bays and open water did not vary significantly, with means showing broad confidence limits at 95 %, ± 91 % for open water and ± 48 % for bays. Furthermore, 31 of 42 species are common to both habitats,

TABLE 1. Fish biomass of two habitat types in the Magdalena basin floodplain system and the principal migrating species (source: Kapetsky et al. 1977a) for biomass).

Species	Open water (kg•ha^{-1})$n=14$	Bay (kg•ha^{-1})$n=15$	Principal migrating species
Triportheus magdalenae	9.669	14.391	x
Potamotrygon magdalenae	2.679	15.527	
Plagioscion surinamensis	7.932	10.584	
Hemiancistrus wilsoni	3.378	5.705	
Pimelodus clarias	3.004	6.251	x
Prochilodus reticulatus	4.440	2.681	x
Pseudoplatystoma fasciatum	2.630	3.963	x
Trachycorystes insignis	3.237	3.295	x
Ageneiosus caucanus	1.096	3.061	x
Pterygoplichthys undecimalis	2.591	1.373	
Sternopygus macrurus	0.339	2.561	
Tarpon atlanticus[a]	2.629	0.000	x
Curimata mivartii	1.056	1.390	x
Eigenmannia virescens	0.755	1.334	
Centrochir crocodilii	0.182	1.446	
Petenia kraussii	0.822	0.716	
Roeboides dayi	0.710	0.670	
Leporinus muyscorum	0.509	0.682	x
Loricaria filamentosa	0.316	0.835	
Sorubim lima	0.090	1.000	x
others 22 spp.	7.651	2.300	
Total	55.715	79.765	

[a] Anadromous fish.

TABLE 2. Minimum and median lengths observed at first sexual maturity for 15 fish species of the Magdalena River basin (source: Escobar et al. 1983; except for *P. fasciatum*, Vera y Villegas 1985).

Species	Standard lengths (mm) at sexual maturity			
	Minimum		Median	
	Males	Females	Males	Females
Petenia kraussii	163	144	198	168
Pterygoplichthys undecimalis	245	195	285	268
Hoplias malabaricus	245	235	305	288
Brycon moorei	255	245	375	379
Triportheus magdalenae	145	135	195	209
Sorubim lima	319	299	425	533
Curimata magdalenae	105	105	133	141
Plagioscion surinamensis	155	155	315	377
Prochilodus reticulatus	201	192	267	345
Ageneiosus caucanus	305	295	473	495
Cyrtocharax magdalenae	215	235	267	287
Curimata mivartii	215	215	250	245
Hemiancistrus wilsoni	225	215	367	323
Leporinus muyscorum	185	175	251	282
Pseudoplatystoma fasciatum	—	—	563	770

showing little qualitative difference between the two groups. Some fishes may move from open water to bays during the change from low to rising water conditions, as shown by the decrease in open water biomass in this period (Table 5). This decrease also reflects movements of fish from open water areas into marginally inundated lands. Later in the hydrological cycle, during the period of high water levels, biomass in bays decreased as some fish moved into the floodplain. At the time of falling water levels, biomass averages for bay and open water habitats become nearly equal. On comparing the ichthyomass values estimated for the Magdalena River floodplain system with the values reported for other tropical rivers, the former are relatively low, which might be due to the marked fish migration towards the main channels of the rivers (Welcomme 1979, 1985).

Kapetsky et al. (1976) proposed tentative hypotheses regarding relationships between ichthyomass and limnologic characteristics of floodplain lakes. The lack of carbon may be one factor influencing fish production, as evidenced by the low bicarbonate concentrations and the inverse linear correlation between free carbon dioxide and ichtyomass estimates ($r = -0.62$, Sy•x = 10.92). Other inversely related factors are phosphates ($r = -0.65$, Sy•x = 10.62), nitrates ($r = -0.71$, Sy•x = 9.81), and chlorides ($r = -0.66$, Sy•x = 10.54). Additional information is required to test these relationships.

Fisheries

FAO (1980) estimated a potential yield of 300 kg•ha^{-1}•yr^{-1} based on permanent floodplain, which would give a maximum total yield of 97 800 t•yr^{-1}. This report considered the biomass estimates and their relationship with the existing fishery yield, noting that 47 % of the permanent floodplain was slightly or not exploited at all, and that there were 13 slightly or non-utilized species. Chapman (1978) estimated a mean yield of 40 kg•ha^{-1} for the Magdalena system based on peak flood; this estimate is similar to the yield of 37.5 kg•ha^{-1} for 13 African river floodplain systems, also calculated on the basis of peak flood (Welcomme 1975).

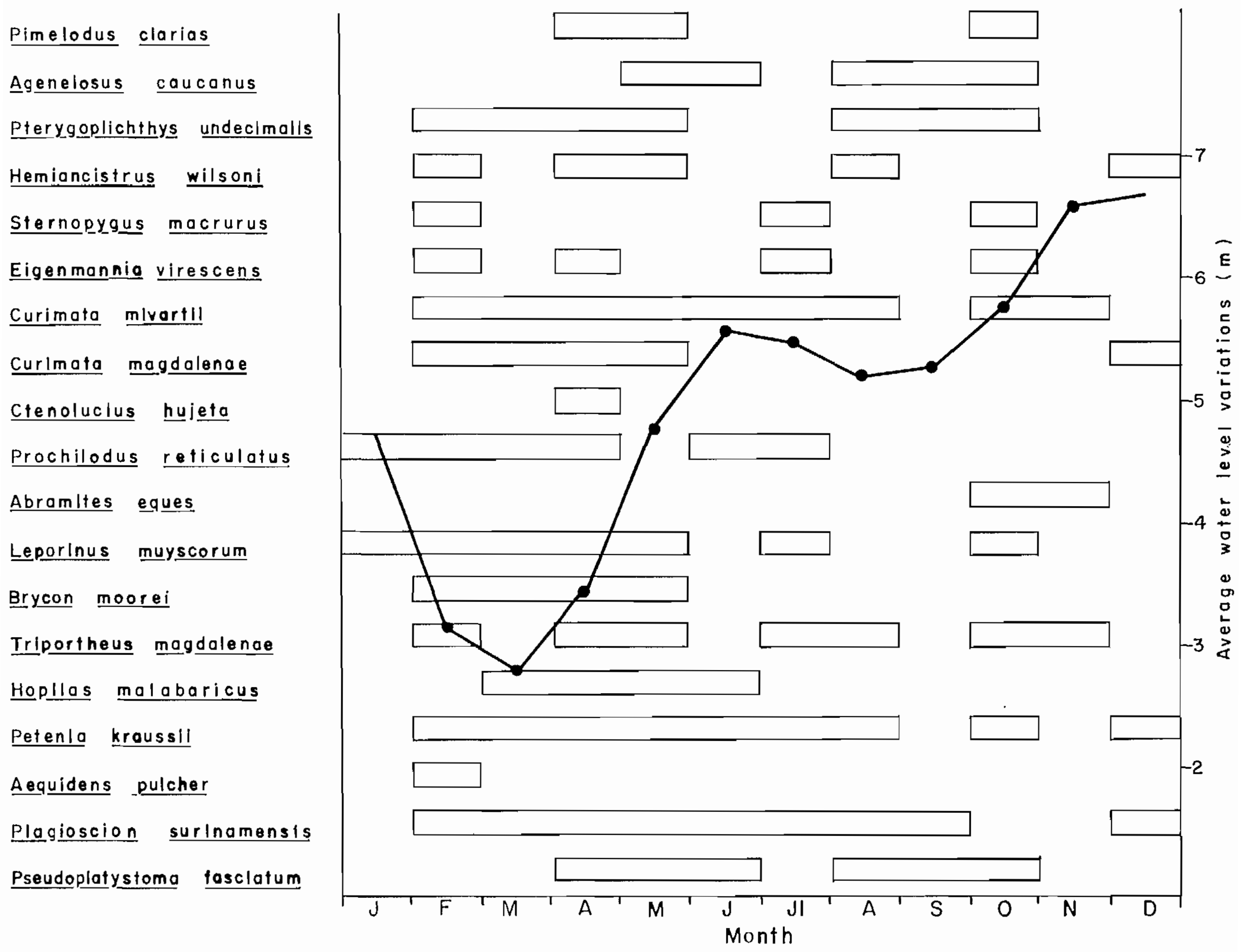

FIG. 2. Fish reproduction periods as evidence by maturity of gonads and presence of juveniles in relation to river water level (source: Kapetsky 1978; except for *P. fasciatum*, Beltrán y Beltrán 1976).

TABLE 3. Physicochemical traits of the Magdalena, Cauca and San Jorge Rivers in the Magdalena River system (source: Ducharme 1975, except for conductivity in the Magdalena River, Arias 1977).

	Magdalena River	Cauca River	San Jorge River
	n=10	n=7	n=2
pH	7.63 (7.40– 7.80)	6.94 (6.50– 7.60)	6.52 (6.50– 6.55)
Turbidity (J.T.U.)	560.70 (155.00–900.00)	1193.70 (500.00–2000.00)	87.50 (55.00–120.00)
Conductivity (μmho•cm^{-1})	166.80 (115.00–230.00)[a]	396.80 (250.00– 500.00)	335.00 (320.00–350.00)
Oxygen (mg•L^{-1})	7.30 (6.00– 9.20)	7.60 (6.00– 8.00)	8.25 (8.00– 8.50)
Carbon Dioxide (mg•L^{-1})	29.00 (8.00– 76.00)	0.00	0.00
Ammonia (mg•L^{-1})	0.00	0.00	0.00
Nitrate (mg•L^{-1})	0.96 (0.25– 4.00)	2.64 (0.16– 8.80)	0.21 (0.16– 0.26)
Phosphate (mg•L^{-1})	0.35 (0.27– 0.50)	0.33 (0.13– 0.65)	0.23 (0.22– 0.24)
Sulphate (mg•L^{-1})	22.00 (5.00– 60.00)	12.70 (7.20– 27.00)	17.00
Silicate (mg•L^{-1})	18.50 (5.00– 26.50)	9.30 (8.00– 10.00)	5.57 (5.15– 6.00)
Alkalinity (mg•L^{-1})	55.70 (45.00– 60.00)	— — —	— — —
Total Hardness (mg•L^{-1})	55.80 (40.00– 75.00)	60.00 (45.00– 65.00)	45.00 (40.00– 50.00)
Iron (mg•L^{-1})	0.07 (0.01– 0.15)	0.93 (0.37– 1.40)	0.54 (0.33– 0.75)
Copper (mg•L^{-1})	0.00 — —	0.46 (0.00– 1.00)	0.20 (0.00– 0.40)
Temperature (°C)	25.30 (24.20– 26.30)	26.50 (25.50– 28.00)	30.27 (29.50– 31.00)

[a] n=5.

TABLE 4. Physicochemical and biological traits of the Magdalena basin floodplain system (source: Kapetsky et al. 1977a; except for primary productivity, Arias 1977; and periphyton, Zárate y Cubides 1977).

	Bays			Open waters		
	$\bar{x}$	r	n	$\bar{x}$	r	n
Color	215.00	40.00 -700.00	13	187.00	35.00 -450.00	13
Turbidity (J.T.U.)	90.00	13.00 -180.00	13	57.00	6.00 -125.00	13
Temperature (°C)	29.70	27.90 - 31.90	14	30.10	27.00 - 32.10	13
Water Level (m)	5.90	4.00 - 8.80	15	5.50	4.10 - 6.40	14
Transparency (cm)	40.00	12.00 -134.00	13	57.00	12.00 -160.00	14
Oxygen (day)	4.70	2.70 - 7.60	13	5.60	2.60 - 8.10	13
Oxygen (night)	4.50	3.00 - 6.40	9	5.30	1.60 - 7.60	12
Carbon Dioxide (mg•7L^{-1})	11.00	0.00 - 20.00	13	11.00	0.00 - 56.00	13
Conductivity (μmhos•cm^{-1})	158.00	85.00 -270.00	15	155.00	85.00 -210.00	14
pH	7.50	6.60 - 8.30	13	7.40	67.00 - 8.50	13
Ammonia (mg•L^{-1})	0.34	0.01 - 1.23	13	0.38	0.00 - 0.96	13
Alkalinity (mg•L^{-1})	54.00	20.00 - 80.00	13	58.00	18.00 - 95.00	13
Hardness ($CaCo_3$)(mg•L^{-1})	42.00	12.00 - 65.00	12	43.00	15.00 - 75.00	13
Total Hardness (mg•L^{-1})	59.00	25.00 - 85.00	13	56.00	18.00 - 80.00	12
Nitrate (mg•L^{-1})	17.40	0.90 - 48.40	13	8.30	0.40 - 37.40	13
Nitrite (mg•L^{-1})	0.18	0.01 - 0.36	12	0.19	0.02 - 0.43	9
Phosphate (mg•L^{-1})	1.85	0.07 - 8.60	13	1.02	0.15 - 7.68	13
Sulphate (mg•L^{-1})	9.00	4.00 - 18.00	10	9.00	0.00 - 17.00	11
Silicate (mg•L^{-1})	13.20	4.50 - 23.00	11	11.50	5.70 - 32.00	11
Iron (mg•L^{-1})	0.80	0.25 - 2.00	13	0.69	0.15 - 1.10	13
Copper (mg•L^{-1})	0.11	0.00 - 0.40	13	0.06	0.00 - 0.13	13
Chloride (mg•L^{-1})	5.10	1.00 - 10.00	13	8.70	2.00 - 10.00	12
Phytoplankton Cells (n°•mL^{-1})	62.20	2.60 -158.70	11	23.60	0.30 -245.40	13
Zooplankton Cells (n°•mL^{-1})	1.50	0.30 - 5.40	11	1.30	0.70 - 3.30	13
Benthos (g•m^{-2})	3.13	1.42 - 4.88	10	1.92	0.06 - 7.02	9
Primary Productivity (gC•m^{-3}•h^{-1})	0.10	0.012- 0.214	14	0.09	0.012- 0.244	18
Periphyton (g•m^{2})[a]	35.14	6.93 -130.72	17			

[a] Wet weight of animals associated to the roots of *Eichhornia* spp.

TABLE 5. Average total fish biomass estimates, in two types of habitat and among water level periods, in the Magdalena basin floodplain system (source: Kapetsky 1978).

Habitat	Water level period	Overall means (kg•ha^{-1})
Bays	low	86.7
	rising	129.1
	high	22.8
	falling	58.3
Open waters	low	127.8
	rising	38.6
	high	—
	falling	43.9

The annual catch in the basin has fluctuated significantly between 1977 and 1985 (Table 6). The first catch and effort assessments were made for the river stratum (Granados 1975). Bazigos et al. (1977) also included the floodplain stratum, but Chapman (1978) used a catch and effort assessment program. This program included intensive and extensive studies throughout the hydrological year following a specific methodology (Chapman et al. 1976), similar to the stratified sampling model designed by Bazigos et al. (1975).

For catch assessment surveys, the basin was divided into seven zones (Fig. 1), and in each one for each hydrological season (presently, only for low water). Two sampling types were used, an extensive sampling, and an intensive and permanent sampling. The extensive sampling included: (a) counting of canoes from an aircraft along the river stratum and in a fraction of the floodplain, i.e. certain "cienagas" (floodplain lakes), (lakes were chosen by nonuniform probability random sampling in which floodplain lake probability values are proportional to their significance and surface area); and (b) field sampling by boat, in which the river stratum and the selected floodplain lakes were studied through direct interviews with the fishery economic units (FEU: canoe, gear(s) and fishermen). Each fishery site was investigated for a period of 24 h. Aerial canoe counting gave effort density and distribution data, measured as canoes•km^{-1} or canoes•ha^{-1}. From the field sampling and effort sampling, effort density information was derived and this was compared with the aerial count results, determining daily catch per FEU and its composition, as well as fishing intensity measured as daily fishing effort.

Subsequently, these data were individually extrapolated by zones, taking into account the total length of the river stratum, including main rivers and tributaries, and the total surface of the floodplain lake stratum, comprising both isolated and river connected lakes. Finally, the total catch per hydrological period, plus the results by zones, were determined and the total annual catch derived from the sum of the total catch per hydrological period.

The intensive sampling for the catch assessment survey was performed at four monitoring centers, located in the

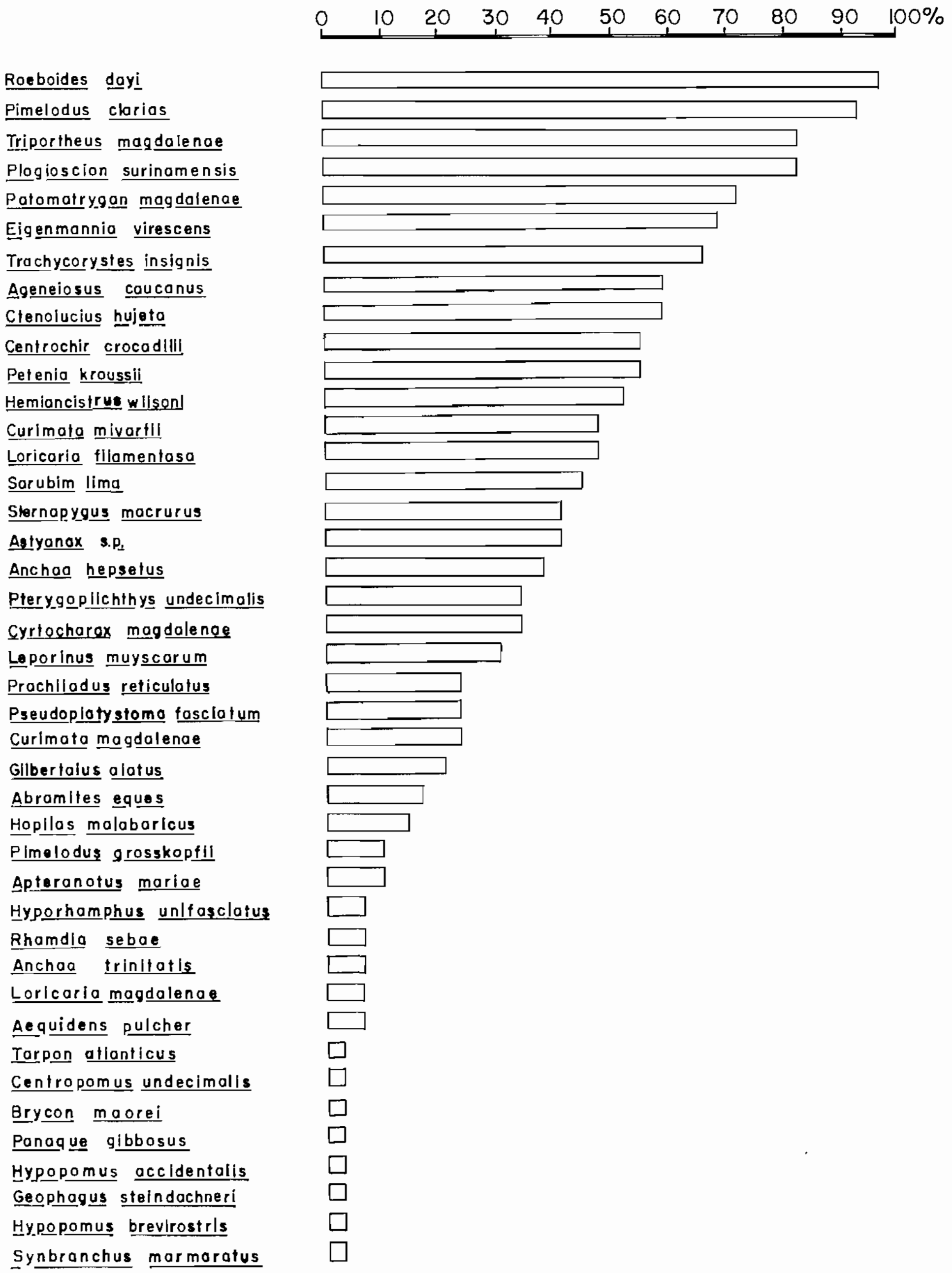

FIG. 3. Fish species occurrence (%) in 29 sampling sites in the Magdalena River floodplain system (source: Kapetsky et al. 1977).

main, middle and lower Magdalena and lower Cauca ports. This sampling is permanent and gives commercial catch data.

The "subienda" low water period (December to March) with 84 fishing days, accounts for an average of 55 % of the total annual catches and is the most important fishery period; the catches in the floodplain represented between 22-42 % ($\bar{x}$ 34 %) of the total "subienda" catch for the period 1977-85. As of 1984, the assessment has been restricted to this period. Estimates since 1981 have shown low catch values compared to the 1977-80 period. Zárate et al. (1983b), correlated the annual catches for the 1977-82 period with the mean annual river levels (r = -0.85), although more statistical evaluation is needed. But, to obtain more exact data, it is necessary to increase the intensity and coverage of the catch assessment program.

In general, water levels have been higher during recent years, and fishing effort decreased, (fishing canoes per day) in rivers. In contrast, the fishing effort in the floodplain showed a fluctuating trend. Figure 4, presents the variation in effort for both rivers and floodplain lakes during the "subienda" period, from 1977 to 1986. Close to 34 000 fishermen work in the basin (FAO 1980).

Different fishing methods are used in the basin; the chief types are the "chinchorro" (seine net) and "atarraya" (cast net) for rivers, and "trasmallo" (gill net) and "atarraya" for floodplain lakes. Other less-used methods are the "barredera" (V-shaped dip net), "cóngolo" (basket-like dip

TABLE 6. Total annual catch and catches for the low water period ("subienda") in the Magdalena River basin, 1974–85.

Year	Subienda catches (t)	Total annual catch (t)	References
1974	25 854[a]	—	Granados (1975)
1975	17 510[a]	—	Granados (1975)
1977	43 134	75 313[b]	Chapman et al. (1977); Chapman (1978)
1978	34 415	64 167	Valderrama et al. (1978); Zárate et al. (1983b).
1979	27 381	49 020	Zárate et al. (1983b)
1980	39 363	64 941	Zárate et al. (1983b)
1981	12 091	25 052	Arias et al. (1981); Zárate et al. (1983b).
1982	20 683	43 780	Arboleda et al. (1982); Zárate et al. (1983b).
1983	20 188	36 869	Arboleda et al. (1983a, b, c); Zárate et al. (1983a).
1984	13 730[c]	—	Arboleda et al. (1984)
1985	19 244[c]	—	Zárate y Martínez (1985)

[a] Not including floodplain catches.

[b] Low estimate from Chapman 1978. He gave a high estimate of 81 000 t, and yield = 40 $kg \cdot ha^{-1} \cdot yr^{-1}$.

[c] Catch assessments have been carried out only during "la subienda".

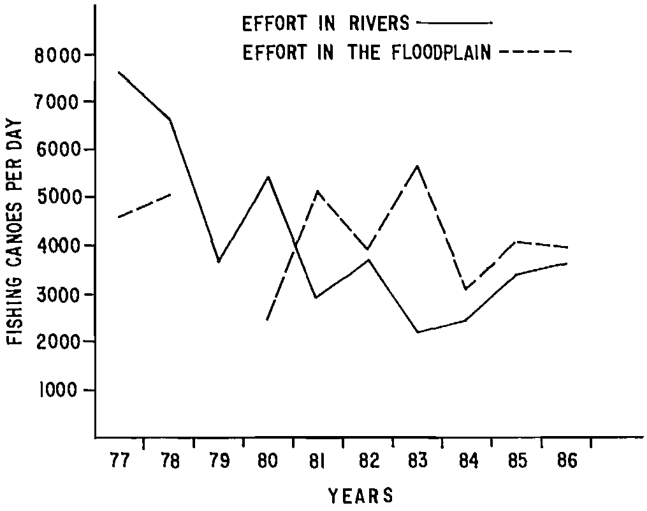

FIG. 4. Fishing effort in rivers and floodplain for the low water period *La subienda*, in the Magdalena River basin (Source: after Arboleda et al. 1984).

net) and "nasa" (fish trap). Recently some methods have spread into the floodplain, the main one being "chinchorro" (seine net). Lately, some types of drift nets are being used in rivers for fishing during high waters; and regulations for their use are presently under study.

The catch per fishing unit indicates that in past years the seine net has been the most effective gear for the river, while the cast net and the set gill-net are the most common ones for the floodplain lakes. However, since 1985 the "chinchorra" (seine net) has spread to the floodplain. During 1985, in the "subienda" this gear captured an average of 84 $kg \cdot d^{-1}$, the highest average catch per fishing unit in the basin (Table 7).

Wahle et al. (1982) identified 26 species of commercial importance. *Prochilodus reticulatus* is fished in both rivers and floodplain lakes, while the *Pseudoplatystoma fasciatum* is caught mainly in rivers (Table 8). Figure 5 shows the median catch length for several commercial species. The catfish *Pseudoplatystoma fasciatum* is caught at small sizes in comparison with the median sizes at maturity (Table 2), a cause for concern for this species. Gill nets, and the general adoption of new fishing methods, appear to affect this species particularly.

Prochilodus reticulatus and *Pseudoplatystoma fasciatum* are the most important species, together accounting for 57 % of the "subienda" catches. *P. reticulatus*, a characid averaging about 0.5 kg, feeds on detritus while *P. fasciatum* is a predatory pimelodid reaching sizes up to 1.5 m. Chapman (1978) determined a 50 % total annual mortality rate for *P. reticulatus*, using the method described by Ssentongo and Larkin (1973), but concluded that this species was not overfished. Information regarding age is presently improving; an example is the study by De Fex (1983) which has begun to provide more precise data. Wahle (1984) has determined a 55 % total annual mortality rate for *Plagioscion surinamensis* which in part led to the introduction of the gill-net in the basin, as this species represented an underutilized stock.

Management Strategies

Because of the artisanal character of the fisheries in the basin, measures to control fishing effort have been directed only towards establishing bans on fishing in the channels between the floodplain and the rivers, and also among the floodplain lakes, as well as restricting the use of gill nets in the floodplain during the April–November high-water season. The effects of seine nets in the floodplain are presently being studied, since this recently adopted method is causing serious conflicts with cast net fishermen.

Another fishery management tool is to regulate the fish length in the catch. Based on the determination of minimum and median lengths at maturity for the main fish species of commercial importance (see Table 2), regulations were established for minimum catch length. Selective studies on set nets, (Granados and Escobar 1977; Escobar and Gómez 1978) have been performed. The potential of this method to increase fishery production in the floodplain was assessed (Kapetsky et al. 1977b). Unfortunately, their uncontrolled use is creating problems by reducing the median catch length of some species. At present, the possibility of establishing a temporary ban for fishing *Pseudoplatystoma fasciatum* is under study.

TABLE 7. Catch per fishing unit for the last five years in Magdalena basin–floodplain system, during "*la subienda*" low water period; and characteristics of principal gears.

Year	Catch per fishin unit over 24 h[a] ($kg \cdot d^{-1}$)					Authority
	Rivers		Floodplain			
	Seine net Chinchorro	Cast net Atarraya	Cast net Atarraya	Set net Trasmallo	Seine net Chinchorra	
1981	41	21	21	—	30	Arias et al. (1981)
1982	57	20	17	14	93	Arboleda et al. (1982)
1983	87	28	27	14	—	Arboleda et al. (1983)
1984	44	21	25	20	44	Arboleda et al. (1984)
1985	31	29	13	18	84	Zárate y Martínez (1985).

Gear	Average sizes	Observations
Seine net	50–80 m × 1.5–2 m	authorized in rivers
Chinchorra	5 cm stretched mesh	
Seine net	70–90 m × 2–3 m	
Chinchorra	5–10 cm stretched mesh	not authorized yet (in evaluation)
Cast net	4–4.5 m diameter	authorized in rivers and floodplain
Atarraya	5–7 cm stretched mesh	
Set net	100–200 m × 4 m	authorized in floodplain for high
Trasmallo	10 cm stretched mesh	water periods.

[a] CPFU: Total mean by zones.

TABLE 8. Fish composition of the catches during "la subienda" low water period for four years, in the Magdalena River basin. (*r* = rivers, *c* = floodplain lakes.)

Species	1977 %		1978 %		1983 %		1985 %	
	r	*c*	*r*	*c*	*r*	*c*	*r*	*c*
Prochilodus reticulatus	12	46	21	40	17	57	39	52
Pseudoplatystoma fasciatum	51	5	39	7	55	4	20	2
Ageneiosus caucanus	6	0	7	1	2	2	3	4
Plagioscion surinamensis	9	5	6	7	6	6	5	20
Sorubim lima	6	4	7	3	7	1	9	1
Pimelodus clarias	—[a]	—[a]	6	2	—[a]	—[a]	8	—[a]
Other	16	40	14	40	13	30	16	21
Authority	Chapman (1978)		Valderrama et al. (1978)		Arboleda et al. (1983a)		Zárate y Martínez (1985).	

[a] This species is included in other.

There are two types of investigations for fishery management: the fishery assessment and the monitoring program. Catch assessment is carried out during the main fishing season i.e. the "subienda", or low water period. Effort and yield data provide historical comparisons of catch and catch per unit effort. Monitoring programs give supplementary information, useful to determine the fishery status and the stage of development. These programs are carried out in four important ports (Fig. 1): Magangué and El Banco in Zone 3, lower Magdalena, Barrancabermeja in Zone 2, middle Magdalena; and Caucasia in Zone 7, lower Cauca. Information regarding quantity and local commercial catch composition is obtained at these ports, as well as biological information, such as fish sizes in the catch, and sizes at maturity. Basic biological studies are also underway. Ageing studies have been intensified to obtain data to determine annual mortality rates for the main species, in accordance with recommendations given by Chapman (1981). More knowledge has been obtained on *Prochilodus reticulatus*, and studies on *Pseudoplatystoma fasciatum* are expected to begin shortly because these species are the most important ones for the Magdalena basin fishery.

In the Magdalena River basin fisheries, the use of complex mechanistic model, e.g. Beverton and Holt (1957), is not practical, and the Graham and Schaefer surplus yield model (Ricker 1975) (density dependent) has certain limitations. At the moment the possibility of using relationships between yield, and edaphic, hydrologic and other factors in order to define predictable relations (density independent) is being evaluated, keeping in mind that practical results have already been obtained (See Welcomme (1976) for African rivers, Novoa (1982) for the Orinoco River, and Petrere (1983) for some rivers in the Amazon River basin).

The chief fishery management problem in the Magdalena

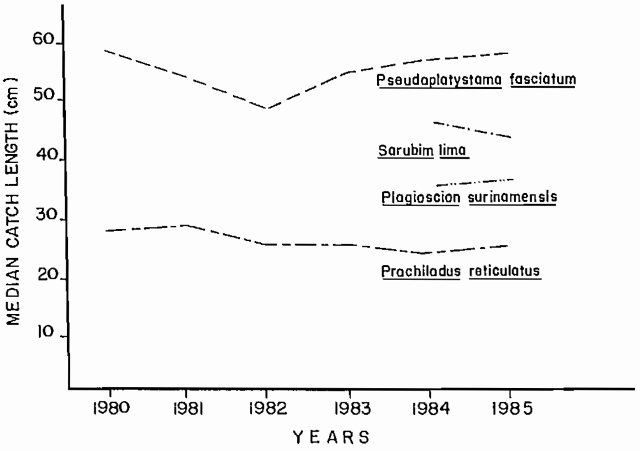

FIG. 5. Median catch length for four species with commercial importance in the Magdalena River basin (Source: Arboleda et al. 1984; Vera y Villegas 1986; and Moreno 1986).

basin is the difficulty in applying technical recommendations, the ultimate aim of which is to guarantee a sustained yield. The artisanal fishery, given its particular characteristics reflected in an economical and social reality of a developing country like Colombia, is neither significantly nor efficiently receptive to technical fishery management strategies suggested. Consequently, in order to stimulate the direct participation of fishermen to put into practice various management strategies, organization of the fishing villages is being heavily promoted. With these measures, the current situation should improve and the organized communities can become the basis for future development programs directed towards another primary objective — socioeconomic development of fishermen.

Some steps have been taken to increase the yield through developments in aquaculture. There are 13 research stations and production centers, 5 in the cool uplands, 3 in temperate areas, and 5 in the warm lowlands. An aquaculture research program has been proposed (Fondo Colombiano de Investigaciones Científicas Francisco José de Caldas, and Instituto Nacional de los Recursos Naturales Renovables y del Medio Ambiente 1985). These centers work mainly on 5 native and 5 exotic fish species. Among the former are cachama, *Colossoma* spp., a transplanted Orinoco species, and mojarras, *Petenia* spp. Among the latter, the Nile tilapia *Oreochromis niloticus* and the trout *Salmo gairdneri* are presently the most important, although freshwater shrimp *Macrobrachium rosembergii* culture shows great prospects for the median term.

Aquaculture production in the basin reached approximately 860 t in 1985. Although these are only partial statistics, *S. gairdneri* contributed with 47 % and *O. niloticus* 34 %, according to statistics by the Aquaculture Division of the Instituto Nacional de los Recursos Naturales Renovables y del Ambiente. At present, plans promoting fisheries in dammed lakes are under way, for example in the Embalse del Guájaro (16 000 ha), located at the lower part of the basin, where a yield of 82 $kg \cdot ha^{-1}$ (Zárate et al. 1986) has already been obtained through repopulation and introduction of new species. Aquaculture programs are also being scheduled for the floodplain to increase yields.

Environmental studies are required to measure the impacts of different activities in the basin. Technical and political steps are being proposed to ensure strict compliance with environmental protection — especially with any activity that might change the hydrological regime of the rivers and their floodplains.

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References

ARBOLEDA, S., P. ARIAS, M. ZÁRATE, G. VERA, Y M. BARRIOS. 1982. Evaluación del esfuerzo y la captura pesquera en el río Magdalena y su plano inundable, La Subienda 1982. Informe Técnico, INDERENA, San Cristóbal. 33 p.

ARBOLEDA, S., P. ARIAS, M. ZÁRATE, G. VERA, AND Y.M. BARRIOS. 1983a. Evaluación del esfuerzo y la captura pesquera en la cuenca Magdalénica, La Subienda 1983. Informe Técnico, inédito, INDERENA, San Cristóbal, 30 p.

———— 1983b. Evaluación de la captura y esfuerzo pesquero en la cuenca Magdalénica y el sistema de plano inundable, Bajanza 1983. Informe Técnico, inédito, INDERENA, San Cristóbal. 16 p., tab.

ARBOLEDA, S., M. ZÁRATE, G. VERA, Y C. MORENO. 1984. Evaluación del esfuerzo y la captura pesquera durante la Subienda 1984 en la cuenca del río Magdalena, y análisis del estado actual de sus pesquerías. Informe Técnico, inédito, INDERENA, San Cristóbal. 39 p.

ARIAS, P. 1977. Evaluación limnológica de las planicies inundables de la cuenca norte del río Magdalena. Publicación del Proyecto INDERENA-FAO, Cartagena. 78 p.

ARIAS, P., M. ZÁRATE, G. VERA, S. ARBOLEDA, Y M. BARRIOS. 1981. Evaluación del esfuerzo y la captura pesquera en el río Magdalena y su plano inundable, Subienda 1981. Informe Técnico, inédito, INDERENA, San Cristóbal. 29 p.

BAYLEY, P. B. 1973. Studies on the migratory characin *Prochilodus platensis* Holmberg, 1889 (Pisces: Characoidea) in the R. Pilcomayo, South America. J. Fish. Biol. 5: 25-40.

BAZIGOS, G. P., J. M. KAPETSKY, AND J. GRANADOS. 1975. Integrated sampling designs for the complex inland fishery of the Magdalena River — basin. FAO, FI:DP/COL/72/552, Working Paper No. 4, Rome. 30 p.

BAZIGOS, G. P., J. M., KAPETSKY, J., GRANADOS, AND J. ESCOBAR. 1977. The present state of the fishery of the Magdalena River basin, FAO, FI:DP/COL/72/552. Working Paper No. 2, 30 p.

BELTRÁN E. DE, Y C. G. BELTRÁN. 1976. Contribución al conocimiento de la biología del bagre pintado (*Pseudoplatystoma fasciatum* Linnaeus, 1766) y su importancia pesquera. INDERENA, Medellín, pag. irr.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the Dynamics of Exploited Fish Population. U. K. Min. Agric. Fish., Fish Invest. (ser. 2) 19: 533 p.

CHAPMAN, D. W. 1978. Total harvest and economic value of the fishery in the río Magdalena and floodplain system. Final Report to FAO/COL/72/552, Cartagena, 68 p.

———— 1981. Practical fisheries assessment in a tropical floodplain. Fisheries 6(3): 2-6.

Chapman, D. W., J. M. Kapetsky, J. J. Escobar, P. A. Arias, y M. Zárate. 1976. Metodología para el muestreo y cálculo de los resultados de la evaluación de la pesca en el río Magdalena. Proyecto para el Desarrollo de la Pesca Continental INDERENA-FAO. Cartagena. 32 p.

Chapman, D., J. Escobar, P. Arias, M. Zárate, C. Lara, y M. Valderrama. 1977. Evaluación de la captura en el río Magdalena y su plano inundable, La Subienda.Informe Técnico, Proyecto INDERENA-FAO, Cartagena. 27 p.

Comision de Pesca Continental para América Latina, COPESCAL-FAO. 1984. Informe de la segunda reunión del grupo de trabajo de la Comisión de Pesca Continental para América Latina, sobre recursos pesqueros. Iquitos, Perú. 26-30 de septiembre de 1983. FAO Inf. Pesca 308: 39 p.

Dahl, G. 1971. Los peces del norte de Colombia. Ministerio de Agricultura, Instituto Nacional de los Recursos Naturales Renovables y del Ambiente, INDERENA, Bogotá. 319 p.

Dahl, G., F. Medem, y A. H. Ramos. 1963. El bocachico, contribución al estudio de su biología y de su ambiente. Corporación Autonoma Regional de los Valles del Magdalena y del Sinú. 144 p.

De Fex, R. 1983. Edad y crecimiento del bocachico *Prochilodus reticulatus magdalenae* (Steindachner 1878) en la parte baja del río Magdalena. Tesis, Universidad de Bogotá Jorge Tadeo Lozano, Cartagena, 42 p.

Ducharme, A. 1975. Informe técnico de biología pesquera (Limnología). Proyecto para el Desarrollo de la Pesca Continental, INDERENA-FAO, Pub. No. 4, Bogotá, 42 p.

Escobar, J., y R. Gómez. 1978. Selectividad de trasmallos para las especies "perro" (*Hoplias malabaricus*) y "mojarra amarilla" (*Petenia kraussii*) en las ciénagas del bajo Magdalena. Informe técnico, inédito, Proyecto INDERENA-FAO, Bogotá. 43 p.

Escobar, J., M. Zárate, M. Valderrama, C. Lara, y C. Fonseca. 1983. Tallas mínimas y medias de maduración para 14 species ícticas de interés comercial de la cuenca Magdalénica (1978). INDERENA. Revista Divulgación Pesquera, XXI (2): 12 p.

Fondo Colombiano de Investigaciones Científicas Francisco José de Caldas, Instituto Nacional de los Recursos Naturales Renovables y del Ambiente. 1985. Programa Nacional para el Desarrollo de la Acuicultura. COLCIENCIAS-INDERENA, Bogotá. 126 p.

FAO. 1980. Resultados y recommendaciones del Proyecto para el Desarrollo de la Pesca Continental INDERENA-FAO. Informe Terminal, FI: DP/col/72/552, Roma. 90 p.

Granados, J. 1975. Estimaciones de la captura, esfuerzo y población pesquera en los ríos Magdalena, Cauca y San Jorge. Proyecto para el Desarrollo de la Pesca Continental, INDERENA-FAO. Publicación No. 18. Bogotá, 103 p.

Granados, J., y J. Escobar. 1977. Selectividad de trasmallos para las especies "pacora" (*Plagioscion surinamensis*) y "bocachico" (*Prochilodus reticulatus*) en las ciénagas del Bajo Magdalena (Colombia). Informe Técnico, inédito. Proyecto INDERENA-FAO, Bogotá. 48 p.

Hurtado, N. 1972. Aspectos biológicos del medio-alto Magdalena, p. 10-44. *En* INDERENA, Operación Subienda 1972, Investigación Pesquera, Bogotá.

Instituto Nacional de los Recursos Naturales Renovables y del Ambiente (Inderena). 1981. Información General Cuenca río Magdalena, Problemática y Políticas de Recuperación y Desarrollo. Ministerio de Agricultura INDERENA, Bogotá, pag. irr.,

1984. La cuenca Hidrográfica del río Magdalena y las acciones del INDERENA en la misma. Proyecto Cuenca Alto Magdalena — PROCAM. Bogotá. 39 p.

1985. Estadísticas pesqueras, Subgerencia de Pesca y Fauna Terrestre, Bogotá, pag. irr.

Julius Berger Konsortium. 1926. Memoria detallada de los estudios del Río Magdalena, obras proyectadas para su arreglo y resumen del presupuesto. Editorial Minerva, Bogotá. 336 p.

Kapetsky, J. M., J. Escobar, P. Arias, y N. Raul. 1976. Evaluación preliminar de la limnología y de las poblaciones de peces en los planos inundables del Canal del Dique, parte II: Poblaciones de Peces. Proyecto INDERENA-FAO, Cartagena. 48 p.

Kapetsky, J. M., J. Escobar, P. Arias, y M. Zárate. 1977a. Algunos espectos ecológicos de las ciénagas del plano inundable del Magdalena. Proyecto INDERENA-FAO, Bogotá. 28 p.

Kapetsky, J. M., D. W. Chapman, J. J. Escobar, P. A. Arias, y M. Zárate. 1977b. El potencial del trasmallo para aumentar la producción pesquera de la ciénagas del río Magdalena. Informe Técnico, Proyecto para el Desarrollo de la Pesca Continental, INDERENA-FAO, Cartagena. 17 p.

Kapetsky, J. M. 1978. Reporte final sobre poblaciones de peces y pesquerías de la cuenca del río Magdalena, Colombia. Proyecto para el Desarrollo de la Pesca Continental. INDERENA-FAO, Cartagena. 17 p.

Kaufmann, R., y F. Hevert. 1973. El régimen fluviométrico del río Magdalena y su importancia para la ciénaga Grande de Santa Marta. Mitt. Inst. Colombo Alemán. Invest. Cien. 7: 121-137.

Lowe-McConnell, R. H. 1975. Fish communities in tropical freshwaters. Longman, London. 337 p.

Mejía, Millán, y Perry Ltda. 1983. Estudio Nacional de Aguas. Departamento Nacional de Planeación Nacional. Informe Principal, Informe Final, Primera Fase, Vol. I, Bogotá. 174 p.

Mikkola, H. 1976. Contaminación del río Bogotá y su influencia en la calidad del agua del río Magdalena. Proyecto INDERENA-FAO, Bogotá. 17 p.

Mikkola, H., y P. Arias. 1975. Evaluación preliminar de la limnología y de las problaciónes de peces en el sistema del Canal del Dique, Parte I. Proyecto INDERENA-FAO. 61 p.

Miles, C. 1971. Los peces del río Magdalena (a field book of Magdalena fishes). Universidad del Tolima, 2a. Ed., Ibagué. 214 p.

Moreno, C. 1986. Informe de monitoreo pesquero y comercialización en Barrancabermeja. Informe Técnico, inédito, INDERENA. 5 p.

Novoa, D. R. 1982. Análisis Histórico de las Pesquerías del Río Orinoco, p. 21-49. *En* D. F. Novoa, (comp.) Los Recursos Pesqueros del Río Orinoco y su Explotación. Corporación Venezolana de Guayana, Caracas.

Pardo, G. 1976. Inventario y zonificación de la cuenca para fines hidroagrícolas, p. D3-1 a D3-7. *En* Conferencias del Foro, Seminario Foro sobre Aprovechamiento Múltiple contra Inundaciones, Proyecto Cuenca Magdalena — Cauca, Convenio Colombo Holandés, Bogotá.

Petrere, M. 1983. Relations among catches, fishing effort and river morphology for eight rivers in Amazonas State (Brazil) during 1976-1978. Amazoniana VIII (2): 281-296.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish population. Bull. Fish. Res. Board Can. 191: 362 p.

Ssentongo, G. W., and P. A. Larkin. 1973. Some simple methods of estimating mortality rates of exploited fish population. J. Fish. Res. Board Can. 30(5): 695-698.

Universidad Nacional. 1985. Diagnóstico del impacto ambiental del Proyecto Hidroeléctrico de Betania, Bogotá. Vol. I: 131 p.

Uries, J. de. 1976. Contexto socioeconómico de la cuenca Magdalena — Cauca, p. A3-1 a A3-10. *En* Conferencias del Foro, Seminario Foro sobre Aprovechamiento Múltiple contra Inundaciones, Proyecto Cuenca Magdalena — Cauca, Convenio Colombo Holandés, Bogotá.

VALDERRAMA, M. B. 1985. Embalses y problématica pesquera. COLCIENCIAS, Revista Colombia: Ciencia y Tecnología 2(3): 11–14.

VALDERRAMA, M., C. LARA, J. ESCOBAR, B. WHALE, Y J. RUD. 1978. Evaluación de la captura en el río Magdalena y el sistema del plano inundable, La Subienda 1978. Informe Técnico, inédito, Proyecto INDERENA–FAO, Cartagena. 22 p.

VERA, G., Y E. VILLEGAS. 1985. Informe anual sobre investigacion básica de pesca y comercializacion de recursos pesqueros en la parte baja de la cuenca Magdalénica, centro de acopio Magangué, durante — 1984. Informe Técnico, inédito. INDERENA, Magangué. 103 p.

1986. Informe anual sobre investigacion básica de pesca y comercialización de recursos pesqueros en la parte baja de la cuenca Magdalénica, centro de acopio Magangué, durante 1985. Informe Técnico, inédito, INDERENA, Magangué (en preparación).

WAHLE, B. 1984. Observaciones preliminares para la determinación de la edad de la pacora *Plagioscion surinamensis* Bleeker (Pisces: Sciaenidae) a partir de los incrementos diarios de crecimiento en los otolitos. Informe Técnico, INDERENA, Bogotá, 18 p.

WAHLE, B., J. VERRETH, Y J. RUD. 1982. La socioeconomía de la pesca del río Magdalena y su sistema del plano inundable (1978). INDERENA, Revista Divulgación Pesquera XIX (3): 16 p.

WELCOMME, R. L. 1975. The fisheries ecology of African floodplains. CIFA Tech. Pap. 5: 51 p.

1976. Some general and theoretical considerations on fish yield of African rivers. J. Fish. Biol. 8: 351–364.

1979. Fisheries ecology of floodplain rivers. Longman Inc., New York, NY. 317 p.

1985. River Fisheries. FAO Fish Tech. Pap. 262: 330 p.

ZÁRATE, M Y A. CUBIDES. 1977. Estudio ecológico de la orilla de las ciénagas del plano inundable del río Magdalena. Publicación del Proyecto para el Desarrollo de la Pesca Continental. INDERENA–FAO, Cartagena. 45 p.

ZÁRATE, M., ET AL. 1983a. Evaluación de la captura y esfuerzo pesquero en la cuenca del río Magdalena y su sistema del plano inundable, La Subienda de Mitaca. 1983. Informe Técnico, inédito, INDERENA, San Cristóbal. 16 p.

1983b. Situación actual de la pesquerías de la cuenca Magdalénica con base en datos de estuerzo y captura 1977–1982. Informe Técnico, inédito. INDERENA, San Cristóbal. 37 p.

ZÁRATE, M., Y J. MARTÍNEZ. 1985. Captura y esfuerzo pesquero presente en la cuenca del río Magdalena y su sistema del plano inundable durante la Subienda 1985, y estado actual de sus pesquerías. Informe Técnico, inédito, INDERENA, San Cristóbal. 16 p.

ZÁRATE, M., J. MARTÍNEZ, Y F. SANCHEZ. 1986. Evaluación de la captura, esfuerzo y comercializacion de recursos pesqueros en el embalse de El Guájaro durante el año comprendido entre marzo 1984 y febrero 1985. Informe Técnico, inédito, INDERENA, San Cristóbal. 27 p., tab., fig.

The Multispecies Fisheries of the Orinoco River: Development, Present Status, and Management Strategies

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Abstract

Novoa, D.F. 1989. The multispecies fisheries of the Orinoco River, development, present status, and management strategies, p. 422–428. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

A brief description of the history, location, uses, morphometry, hydraulics, ecology, fisheries and management of the Orinoco River is provided. The river has a total length of 2 140 km and an area of 950 000 km^2. The mean annual flow rate is 30 945 m$^3 \cdot$ s^{-1}.

Orinoco's fish community is diverse and the commercial fisheries include about 60 species. This multispecies fishery has been growing since the early 1970's. Actual landings are about 12 000 tons. This is lower than the estimated potential of 45 000 tons. The increase in fishing intensity has induced changes in the species composition of the catch, especially in heavily exploited areas. Piscivores have been replaced by high yield, fast growing species like *Prochilodus mariae*.

Variations in flood intensity have remarkable effects on this species' abundance and catches, as well as on the rest of the fish community. Similar analyses of other sectors of the Orinoco system failed to derive such a clear relationship.

The coexistence of different situations must be taken into account in the definition of management strategies. The proposal is to reinforce the present tendency and to manage the fishery on a high yield basis in those areas with high fishing pressure. Areas less exploited and dominated by polyannual species could be managed to conserve the present species composition and the highest diversity of the community.

Résumé

Novoa, D.F. 1989. The multispecies fisheries of the Orinoco River: development, present status, and management strategies, p. 422–428. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

On donne une brève description de l'histoire, de l'emplacement, des utilisations, de la morphométrie, de l'hydraulique, de l'écologie, des pêches et de la gestion du fleuve Orénoque. Le fleuve s'étend sur une longueur totale de 2 140 km et a une superficie de 950 000 km^2. Son débit annuel moyen est de 30 945 m$^3 \cdot$ s^{-1}.

La communauté de poissons de l'Orénoque est diversifiée et environ 60 espèces font l'objet d'une pêche commerciale. Cette pêche polyvalente est en essor depuis le début des années 70. Les débarquements réels sont d'environ 12 000 tonnes. Ce chiffre est inférieur au potentiel estimé à 45 000 tonnes. L'accroissement des activités de pêche a modifié la composition des espèces formant les prises, particulièrement dans les secteurs fortement exploités. Les espèces piscivores ont été remplacées par des espèces à croissance rapide et à rendement élevé comme *Prochilodus mariae*.

Les variations d'amplitude des inondations ont des effets remarquables sur l'abondance et les prises de cette espèce, de même que sur le reste de la communauté de poissons. On n'a pu tirer d'analyses similaires d'autres secteurs du bassin de l'Orénoque une relation aussi claire.

Il faut tenir compte, dans la définition des stratégies de gestion, du fait qu'il existe des situations différentes. On propose de renforcer la tendance actuelle et de gérer la pêche en fonction d'un rendement élevé dans les secteurs où la pression de pêche est forte. Les secteurs moins exploités et dominés par des espèces polyannuelles pourraient être gérés de façon à conserver la composition actuelle des espèces et la plus grande diversité de la communauté.

History

Thousands of native people live along the Orinoco River in small villages. For centuries they have used the river for navigation and exploited its natural resources.

On his third voyage in 1498, Christopher Columbus, discovered the mouth of the Orinoco. Diego de Ordaz, in 1531, was the first Spaniard to explore the main channel penetrating 800 km upstream to the Atures and Maipures rapids. Many other adventurers, including Antonio Berrio and Francisco Bobadilla, mounted expeditions up the Orinoco looking for "El Dorado".

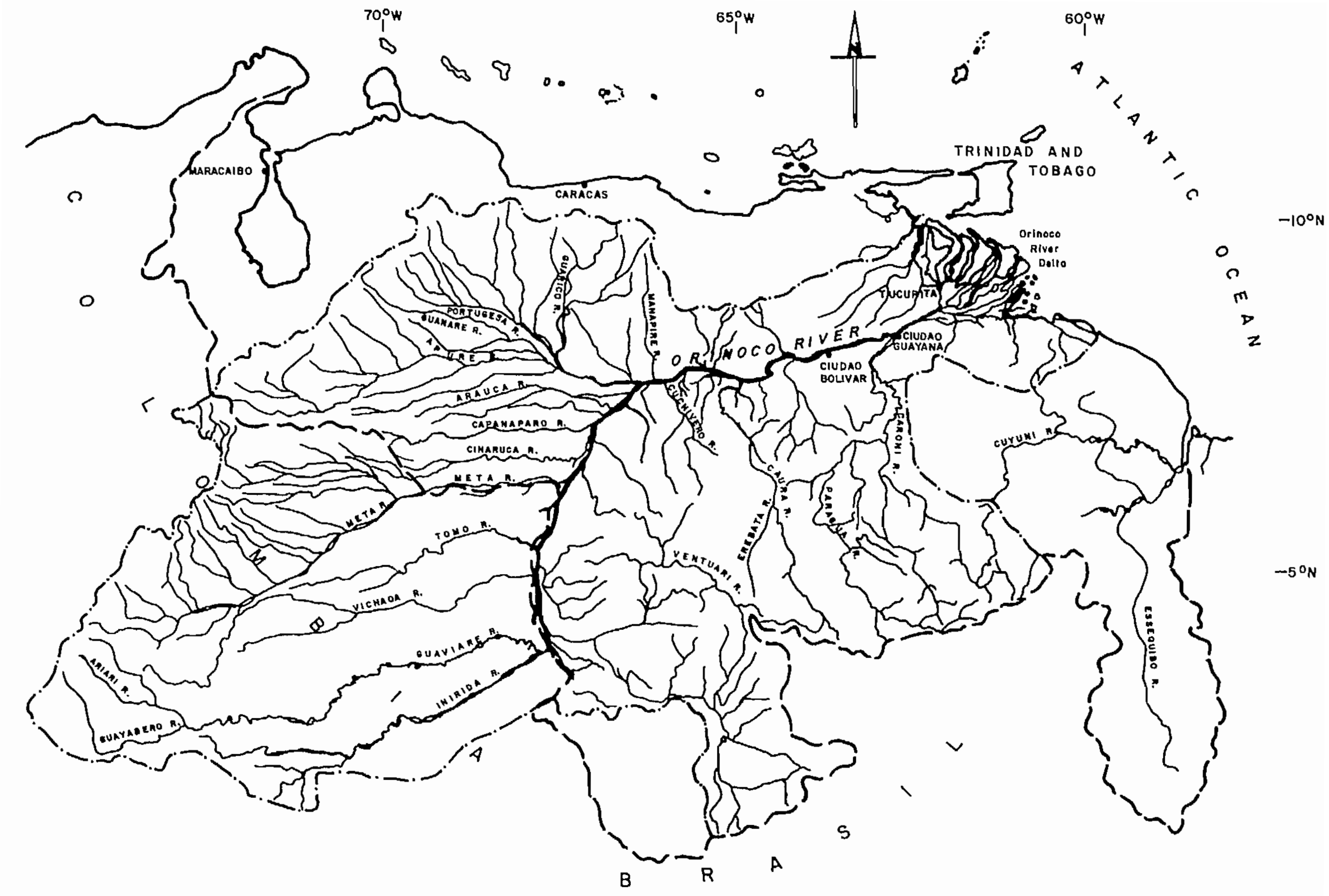

FIG. 1. The Orinoco River Basin.

After the "conquistadores", the rivers of the Orinoco basin were penetrated by missionaries, especially Jesuits and Capuchin monks seeking to convert the native populations.

During the seventeenth century there was an intensification of religious activity and the establishment of numerous small villages and towns leading to a rapid growth of trade along the river.

The chronicles of some missionaries provide an interesting account of the habits and traditions of the native people living along the river.

After the War of Independence, the Orinoco River was explored by naturalists and scientists who accumulated useful collections and studies of the fauna and flora of the river. Particularly interesting were the expeditions and studies of A. Humbolt, between 1800 and 1804. In 1951, the Venezuelan Government supported an official expedition which, finally, discovered the headwaters of the river.

Location

The Orinoco River is situated in Venezuela, South America. The headwaters are located at the southern part of this country, at the Brazilian border, at 2°10′N and 64°20′W approximately, in the Parima and Unturan Mountains. From here the river runs northeast, crossing the middle part of Venezuela and discharging into the Atlantic Ocean through a wide delta, located between 8°35′ and 10°05′N and 61°20′ and 62° 25′ W (Fig. 1).

Uses

Traditionally, the Orinoco River has been used by fishermen and part-time farmers to produce fish and for draw-down agriculture to produce short-term crops. The fishermen utilize the main channel and the lagoons of the floodplain. The farmers clear the brush from low-lying land after the floods and seed a variety of plants. The cropping season lasts about 3–4 months.

The river has also been used for navigation by the riverine people for carrying their products to the local markets.

During the early 1950's heavy industries developed to exploit different types of minerals, especially iron. port facilities were built on the river and the Rio Grande channel of the Orinoco delta was dredged to facilitate passage of sea-going cargo vessels which now travel 380 km upriver to Puerto Ordaz.

Recently, user demand on the Orinoco River has increased. Water has been used for urban development, but at the same time, cities discharge polluted water without any treatment. The new industrial complexes installed in these cities also have a high water demand.

In the near future the Orinoco River will be the focus of new stresses, stemming from multipurpose projects aimed at the development of the river's hydroelectrical potential, jointly with the exploitation of minerals, and development of navigation and oil resources. The environmental impacts of these projects will be evaluated.

Morphometry

The total length of the Orinoco River is 2 140 km in a basin of 950 000 km^2. The river ranges from 1 to 22 km in width.

The river bed is composed, primarily of sand with grain diameter varying between 0.25 and 0.6 mm. The annual sediment discharge is estimated to be 210 $\times 10^6$ tons. Most sediment is transported to the lower Delta where it is deposited, forming sandy low lands locally known as "barras".

During the dry season, the water level falls 12 m below its maximum height. At that time, the sandy river bed is partially exposed to wind currents which cause important transportation of sediments.

In the headwater zone, the Orinoco flows with a moderate velocity (2–5 km• h^{-1}). Flow is slower in the middle reaches and even slower in the delta zone because of the reduced slope.

In the upper basin, the floodplain area is reduced, but in the middle reaches the Orinoco receives very important tributaries, many of them draining the Andes and running from west to east until their junction with the main stream. Here the Orinoco also receives tributaries from the Guayana shield, whose waters are acidic and poorly mineralized. In this section, the Orinoco has a very wide floodplain which forms an internal "delta" during the high water season. The estimated area of this "delta" is about 70 000 km^2. From this point to the coastal delta, the width of the floodplain is variable and generally narrower.

In the coastal delta, the flooded area is very extensive because the terrain is flat. The area of this low-lying land is estimated at 20 000 km^2. A larger area is influenced by the marine environment through the action of the tides, especially in the northern mouths of the delta.

Energy Flow

Little is known about energy flow in the Orinoco's ecosystems. Probably, as has been recognized for other systems, higher vegetation contributes the major part of the primary production in the Orinoco system and of this grasses appear to play a particularly important role.

Vásquez and Sánchez (1984) reported 62 genera of phytoplankton in the main channel with *Melosira* and *Cyclotella* being the most abundant. The maximum abundance was found in the dry season, between January and March with densities of 53 485 organisms• L^{-1}. During the flood the abundance of phytoplankton was minimal with 429 organisms• L^{-1}. The same pattern was found with zooplankton, with a maximum abundance of 6 000 organisms• L^{-1} during the dry season, between January and April. Rotifers were the most important group with Cladocera and Copepoda also present. One floodplain lagoon was sampled during this study and yielded 42 genera; 22 Chlorophyta, 14 Chrysophyta and 6 Cyanophyta. Maximum density was between February and May with 450 000 organisms• L^{-1}, and the minimum was in September with 429 organisms• L^{-1}. The authors concluded that the abundance of phytoplankton and zooplankton are inversely related to the level of water. The density of phytoplankton was higher in the lagoon than in the main river channel, indicating that current is a limiting factor for the growth of plankton.

A very important source of energy for the aquatic system comes from allochthonous materials, both plant and animal, that fall into the water, especially during the high water period. Several fish species use allochthonous material, such as *Colossoma macropomum*, *Piaractus brachypomus*, *Mylossoma duriventris*, and *Triportheus elongatus*. Some change their food habits to autochthonous food during the dry season. *Piaractus brachypomus*, for example, stops migration upstream periodically for 2–3 days during which time it feeds on invertebrates (*Ephemeroptera*) and small molluscs, probably to recover energy in order to continue migration.

Other groups of fish like the prochilodontids and curimatids feed on micro-organisms, organic decay products and detritus associated with mud. The prochilodontids feed mainly during the high waters. Migrant individuals of this family present in the main channel between September and April have a high percentage of empty stomachs and heavy fat deposits in the tissues. These deposits form the energy source for migration and further sexual maturation.

Another important trophic group in the Orinoco River is that of predatory fishes. The adult stages of almost all the members of the Pimelodidae are carnivores and mainly piscivores. The family includes gigantic catfishes of the genus *Brachyplatystoma*, *Pseudoplatystoma*, *Phractocephalus*, and *Paulicea*. Other carnivorous fishes are also very common in the Orinoco River, including *Pellona flavipinnis, Hydrolycus scomberoides, Plagioscion squamosissimus*, and *Cichla ocellaris*. The detritus feeding "Camarón de río" *Macrobrachium amazonicum* is a common item in the stomach contents of carnivorous fishes, especially in the reaches from the middle Orinoco to the Delta where the shrimp is very abundant.

The most important members of the doradid catfishes in the Orinoco River have different habits. *Pterodoras angelli* is widely distributed in the system, inhabiting the full length of the main channel. It is a predominantly herbivorous species, although invertebrate remains, fish and detritus have all been found in their stomachs. *Oxydoras niger* is also very common. It is an omnivore with a preference for plant remains, insects, shrimps and bivalve molluscs. *Megalodoras irwini* prefer molluscs, mainly gasteropod snails.

Other important families of catfishes, loricariidae and callicthydae have members classified as omnivores, ingesting microorganisms of plant and animal origin associated with macrophytes, rocks, mud and other kinds of substrate.

The definition of the energy pathways in very complex systems such as the Orinoco River is not simple as there are energy fluxes of different origins. Seemingly, however, food webs based on allochthonous inputs have a major importance to the energy flow throughout the aquatic system.

Hydraulics

Although the median annual flow of the Orinoco River is 30 945 m^3• s^{-1}, there is a big difference between flow in the dry and rainy seasons. Figure 2 illustrates the changes in water level of the Orinoco River during the year. As a river with an enormous basin area, the hydrological cycle is regular without extreme short-term variations.

The main channel retains the major part of the water during the dry season, but is connected with the alluvial plain during the flood. The establishment of links with the lagoons is of fundamental importance to the biology of many fish species. The total area flooded by the river depends on the intensity of the rains and the annual flood cycle. I have found some evidence of the effects of these changes on the total production of fish in the system (Table 1).

The width of the floodplain area in the Orinoco River is variable, being maximal in the coastal delta and where the river receives the major affluents from the western part of Venezuela and from Colombia. Both major areas of the Orinoco River have high fishery potential.

Fish Community Composition, Migrations and Distribution

Composition

In 1970, 318 species were described from the Orinoco basin and the number has increased since then. The most important families are the Characidae, Loricariidae and Pimelodidae. The commercial fisheries include about 60 species although no more than 15 constitute the bulk of the catch (Novoa and Ramos 1978).

The species composition of the catch varies depending on the section of the river. In the western section, at the confluence of the Orinoco with Apure, Meta, Arauca and other Colombian tributaries, *Colossoma macropomum* is the most important species, followed by *Pseudoplatystoma* sp., *Plagioscion squamosissimus* and *Piaractus brachypomus*. Down river, where the floodplain is narrower, the catch is dominated by *Prochilodus mariae*, which represents 40 % or more of the total landings. *Pseudoplatystoma* sp., *Plagioscion squamosissimus* and *Semaprochilodus laticeps* also form a significant percentage of the total landings.

Finally, in the delta there are basically two zones: the high-middle delta with *Prochilodus mariae*, *Plagioscion squamosissimus* and *Hoplosternum littoralle* as the most important commercial species and the lower delta with estuarine waters during some months of the year, where the ariid catfishes together with *Piaractus brachypomus*, *Brachyplatystoma* sp., and *Plagioscion squamosissimus* dominate.

Migration

Massive upstream movements are performed by several species of fish in the Orinoco system. The best known of these is *Semaprochilodus laticeps*. From July to September many individuals of this species move laterally from the lagoons of the floodplain to the main channel. They then move upstream looking for spawning areas. *Semaprochilodus kneri* also move upstream during high water.

Another migration, well known to fishermen, is that of *Piaractus brachypomus* which move upstream during February and March, when the Orinoco River is at its lowest level. During movement the frequency of ripe individuals is high. Schools move at least 150 km, stopping for a few days at specified places where the fish find insect larvae and molluscs associated with submerged vegetation and inorganic substrate.

Prochilodus mariae performs massive movements along the main channel during two periods of the year:

(1) September to January, fish move upstream in the dry season, for dispersal. Individual fish have heavy fat deposits, no stomach contents and show no sexual activity.

(2) February to June, when the water level starts to increase, fish move upstream apparently for spawning. The majority of fish are sexually mature at this time.

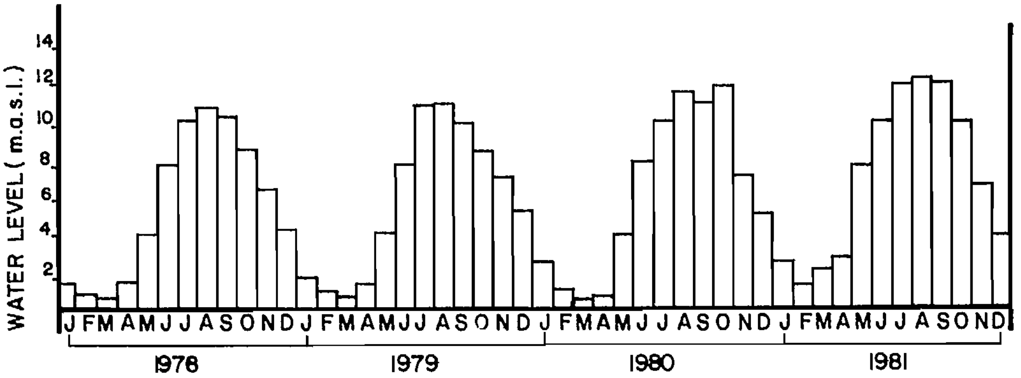

FIG. 2. Seasonal changes in water level of the Orinoco River.

TABLE 1. Regression analysis relating catch, catch per unit effort and hydrological indexes, for Orinoco River.

Variable y	Variable x	Equation	r	n	$P<$
Catch y^a	$0.5H1_y+0.5H1_{y-1}$	$C_y= -634.8+0.53\ (H1_y+H1_{y-1})0.5$	0.62	15	0.05
Catch y^b	$0.5H1_y+0.5H1_{y-1}$	$C_y= -389.4+0.19\ (H1_y+H1_{y-1})0.5$	0.73	10	0.05
$c/f_y{}^b$	$H1_y$	$c/f_y= -179.4+0.18\ H1_y$	0.73	10	0.05

[a] Total catch.

[b] Catch of *P. mariae*.

($H1_y$ = hydrological index year y; C_y = catch year y; c/f_y = CPUE year y.)

From July to September, juvenile fish of various species, mainly prochilodontids, migrate downstream, probably looking for lagoons on the floodplain, which represent their feeding habitats.

Distribution

Many species have a wide range in the river. The most common species of the prochilodontid, pimelodid, loricariid, doradid and characid families, among others, are widely distributed being relatively easy to capture either in lagoons or in the main channel in the lower 800 km of the river (middle and lower sections). Other groups of fishes are also very common like the gymnotids, cichlids, and sciaenids.

I have found remarkable differences in distribution of Orinoquian fish between the main channel and the floodplain. Generally, I can define three main groups of fish:

(1) species that are abundant in both lentic and lotic habitats, thus occupying all available space. *Prochilodus mariae*, *Semaprochilodus laticeps*, *Pseudoplatystoma fasciatum*, *P. tigrinum*, *Plagioscion squamosissimus*, and *Piaractus brachypomum* are representatives of this group,

(2) species whose habitat is restricted to the main channel. *Brachyplatystoma* sp., *B. vaillantii* and *Goslinea platynema* are examples of this category, and

(3) fishes found in the lagoons of the floodplain only. *Cichla ocellaris* and *Hoplias malabaricus* are typical of this group.

Hoplosternum littoralle, *Astronotus ocellatus*, and *Hypostomus* sp., are normally found in secondary channels or blind river arms which behave much as lagoons during dry season. These species are also very common in small lagoons.

Gymnotids are usually found in the deepest zones of the main channel although some species penetrate the lagoons of the floodplain.

Productivity, Standing Stock, Yield and Catch Per Unit Effort

I have no estimates of standing stock in the main channel of the Orinoco River. In small lagoons of the floodplain I have obtained standing stock estimates fluctuating between 1 600 and 2 700 fish• ha^{-1}. Theoretical yield from the Orinoco fishery has been estimated following indirect methods suggested by different authors (Kapetsky 1974; Welcomme 1976, 1979).

Using general morphological data on the fluvial system (basin area, etc.) and some values of yield found in sectors of the river where fishing activity is intense, a theoretical annual yield of 40 000–45 000 t has been estimated for the Orinoco River (Novoa 1982). This estimate will fluctuate depending on the hydrological cycle. Analysis of data on landings for a sector of the Orinoco River showed that the catch per unit effort was significantly correlated with a hydrological index (H1 of Kapetsky 1974). This correlation is even higher when regression analysis is done for annually migratory species of rapid growth, such as *Prochilodus mariae* (Tables 1, 2, and 3). These results suggested that variations of flood intensity have a remarkable effect on the levels of population abundance and catches of *P. mariae*, as well as on the rest of the fish community. In the sector of the Orinoco, where this analysis was performed, *P. mariae* was the most abundant species.

For the same area, a traditional fishery based on *Semaprochilodus laticeps*, showed drastic intra-annual changes in total landings. The variability of the flood intensity seems to be very important to changes of population abundance of *Semaprochilodus*. For it, I have derived a linear equation relating total catch (C) with the hydrological index (H1):

$$\mathrm{C}y = -\ 165.33 + 0.192\ \mathrm{H1}_Y (n = 6, P < 0.10, r = 0.79)$$

Improved catches in the years following years with good flooding are generally attributed to the better survival and growth of fry spawned in the latter years due to an extension of inundated land. Improved catches within years of good flooding (intra-annual correlations) are generally attributed to the greater number of lagoons becoming connected with the river as flood height increases and thus improving opportunities for migration.

Similar analyses done in other sectors of the Orinoco system, which are morphologically different, failed to derive such clear relationships between changes in hydrological index and abundance of fish (Table 4).

TABLE 2. Annual catch rates (kg/fishing trip) for *Prochilodus mariae*, total ichthyomass and the hydrological index (H1) between 1979 and 1985 for fishing areas of the middle Orinoco.

	1979	1980	1981	1982	1983	1984	1985
Prochilodus mariae	19.12	25.24	42.26	46.13	48.97	26.15	17.21
Total ichthyomass	53.50	76.87	66.97	80.00	74.78	61.82	55.39
Hydrological index	2905	3351	3587	3252	3219	2322	2553

TABLE 3. Regression analysis relating annual catch rates (kg/fishing trip) and hydrological index (H1) for *Prochilodus mariae* and total ichthyomass for fishing areas of the middle Orinoco.

Variable y	Variable x	Equation	r	n	P
C/f_y[a]	$0.5\ \mathrm{H1}_y + 0.5\ \mathrm{H1}_{y-1}$	$c/f_y = -59.33 + 0.030\ (\mathrm{H1}_y + \mathrm{H1}_{y-1})0.5$	0.85	7	0.05
C/f_y[b]	$0.5\ \mathrm{H1}_y + 0.5\ \mathrm{H1}_{y-1}$	$c/f_y = -1.48 + 0.026\ (\mathrm{H1}_y + \mathrm{H1}_{y-1})0.5$	0.76	7	0.05

[a] = C.P.U.E. of *P. mariae*.

[b] = C.P.U.E. of total ichthyomass.

TABLE 4. Annual catch rates (kg/day) for *Prochilodus mariae*, *Colossoma macropomum* and total ichthyomass between 1981 and 1984 for the internal delta of the Orinoco River.

	1981	1982	1983	1984	1985
Prochilodus mariae	1.51	2.73	4.30	4.37	8.53
Colossoma macropomum	21.42	17.92	16.57	13.68	16.25
Total ichthyomass	55.54	49.59	50.99	59.75	70.37

TABLE 5. Total landings, total fishing effort and CPUE for the Orinoco River at Ciudad Bolívar, Tucupita and Barrancas fish landings. (Source: Ministerio de Agricultura Y cria dirrécion general de pesca Y avicultura.)

	Landing (t)	Fishing effort (No. boats)	CPUE (t/boat)
1966	1778	258	6.89
1967	1867	—	—
1968	2815	355	7.93
1969	3169	372	8.52
1970	—	—	—
1971	1858	213	8.72
1972	2582	351	7.36
1973	3259	419	7.78
1974	4212	365	11.54
1975	3730	350	10.66
1976	2481	488	5.08
1977	2695	564	4.73
1978	4323	625	6.92
1979	4392	734	5.86
1980	5487	752	7.30
1981	5056	891	5.67
1982	6841	749	9.13
1983	8121	743	10.93
1984	7293	779	9.36

Source: Dirección General de Desarrollo Pesquero (MAC).

The commercial fisheries of the Orinoco River are artisanal in nature. They have been growing since the early 1970's, with increased numbers of boats and total catch. In 1983, reported total landings were 8 121 t, the maximum weight recorded in the last 20 years. Real landings are more probably around 12 000 t yearly, still far from the estimated fishing potential. Table 5 shows the official data on landing and total effort.

The increase in fishing intensity has induced qualitative changes in the species composition of the catch. Those changes are conspicuous especially in some areas already heavily exploited, with high densities of fishermen and narrow floodplain areas. There has been a progressive replacement of carnivorous species at the top of the food web by high yield, fast-growing and bottom-feeding species. Over a significant length of the Orinoco River *Prochilodus mariae* and *Semaprochilodus laticeps* have become the dominant species in the landings. *Plagioscion squamosissimus* and *Pseudoplatystoma* sp., which, although carnivorous, are euryphagous, fast growing, and also important in the fishery. On the other hand, the proportion of *Brachyplatystoma* sp., *Phractocephalus hemioliopterus* and *Paulicea* sp., have been declining in the catch. Neverthe-

TABLE 6. Catch rates (kg/trip) of commercial species from landings in Ciudad Bolívar (middle Orinoco).

Species	1979	1980	1981	1982	1983	1984	1985	1986[a]/
Payara	0.09	0.24	0.05	0.03	0.05	0.19	0.00	0.11
Palometa	1.76	2.76	0.41	1.30	2.31	5.81	4.47	3.98
Coporo	19.12	25.24	42.26	46.13	48.87	26.15	17.21	49.43
Sardinata	0.48	0.12	0.05	0.04	0.10	0.03	—	0.01
Curvinata	8.33	12.53	4.45	11.67	8.28	9.23	6.32	2.43
Bagre Rayao	8.24	16.18	7.39	9.17	7.81	10.41	10.63	3.99
Boca Chico	—	2.43	0.17	—	—	—	—	—
Bagre Lau-Lau	2.00	1.15	1.24	0.91	0.92	1.21	0.48	0.86
Morocoto	1.51	2.81	1.32	1.94	1.96	2.68	4.04	5.26
Cajaro	1.19	0.69	0.65	0.66	0.39	1.47	0.94	2.04
Bagre Dorado	1.11	1.57	0.57	0.57	0.50	0.37	0.69	0.66
Pijotero	0.03	0.01	0.33	—	—	—	—	—
Cachama	1.64	2.01	0.86	0.62	0.72	0.68	0.39	0.13
Bagre Amarillo	0.41	0.21	0.19	0.31	0.29	0.43	0.05	0.14
Mije	0.06	0.02	0.01	—	—	—	—	—
Zapoara	6.18	6.19	5.30	5.87	1.31	2.26	8.89	0.50
Cabo de Hacha	0.14	0.24	0.02	0.05	0.03	0.10	0.10	0.03
Bagre Blanco Pobre	0.10	0.05	0.09	0.35	0.02	—	—	0.04
Guitarrilla	0.11	0.12	0.15	0.07	0.03	0.01	0.17	0.23
Paisano	0.02	0.12	0.00	—	—	—	—	—
Palambra	0.04	0.62	0.24	—	0.63	0.76	0.87	1.86
Blanguita	0.10	0.12	0.14	—	—	—	—	—
Bagre Tigre	0.09	0.05	0.02	—	0.09	—	—	—
Bagre Garbanzo	0.05	0.00	0.02	—	0.17	0.02	0.07	0.04
Doncella	0.08	0.05	0.13	—	0.07	0.00	0.03	—
Various catfish	0.61	1.47	0.91	0.31	0.05	—	0.04	0.48
Total kg/trip	53.53	76.87	66.97	80.00	74.78	61.89	55.39	73.18
Number of trips	913	556	2426	1551	1571	1042	1024	473

[a] Based on January to July.

Source: Corporacion Venezolana de Guayana proyecto de desarrollo pesquero.

less, total catches in this section of the river have increased in the last few years.

In the zone of the Orinoco River around the internal delta there is an important fishery with total landings of 3 000 t per year. A fishery research programme over four years indicated that there have been no significant changes in the species composition of the catch regardless of the magnitude and intensity of exploitation.

Results suggested that the multispecies Orinoco fisheries have evolved in different ways depending on the extent of the floodplain and the various fishing pressures exerted in the different sectors of the rivers (Tables 6 and 7). In some regions of the Orinoco system with limited floodplain and relatively high fishing pressure, gradual changes in species composition of the catch has occurred, tending toward dominance of short cycle, "*r*" type species. On the other hand, in sectors with extensive floodplain and relatively lower fishing pressures, there is no evidence of such changes. Table 8 shows the main differences (morphological and fishing pressure) between both zones. The foregoing comparisons suggest the coexistence of different situations in the same river system which must be taken into account in the definition of policies and management strategies.

TABLE 7. Catch rates (kg/day) by commercial species and total from landings in Caicara.

Species	1981	1982	1983	1984	1985
Curvinata	9.40	4.34	5.73	7.48	7.65
Bagre Rayao	13.93	9.13	5.81	7.78	8.11
Bagre Dorado	3.48	1.59	3.38	2.67	3.25
Bagre Lau-Lau	0.17	0.80	1.26	0.93	1.39
Bagre Cajaro	0.47	0.94	0.74	0.51	0.76
Palometa	1.54	1.37	3.83	10.76	6.70
Cachama	21.42	17.92	14.73	13.68	16.25
Morocoto	2.19	6.77	5.71	4.70	6.96
Coporo	1.51	2.73	4.30	4.37	8.53
Zapoara	0.18	0.70	0.54	0.66	2.50
Bagre Amarillo	0.33	1.26	1.23	1.28	0.63
Bagre Garbanzo	—	1.66	2.70	1.99	2.77
Others	0.92	0.95			4.87
Total	55.54	50.16	49.96	56.81	70.37
No. of days	225.0	682.0	915.5	782.25	678.0

Source: Coporacíon Venezolana de Guayana proyecto de desarrollo pesquero.

TABLE 8. Comparison between two zones of the Orinoco River with different morphological and fishing characteristics.

	Middle zone of Orinoco	Internal delta
Channel length (km)	160	200
Floodplain area (km^2)	640	1500
Fishermen (number)	450-550	400-500
No. of fishermen/km^2	0.7-0.9	0.26-0.33
Km^2 floodplain/km channel	4.0	7.5

Management Practices

The Orinoco River fisheries have been expanding since the last decade despite lack of precise objectives.

The present legal administrative framework aims at the preservation of maximum diversity in the fish community. There are many kinds of regulations related to mesh size of gillnets, prohibition of fishing in floodplain lagoons, minimum size limits, closed seasons among others. In spite of conflicts between fishermen and authorities, fishing is still carried out, often ignoring the rules, thereby producing a no management situation. The social and economic cost of effective enforcement of the present legislation is prohibitive.

For this reason and assuming a continuous growth of the artisanal fishery, different management options are proposed depending on the objectives. If the objectives are to increase food production or employment, then there is an urgent need to change the present conservation policies. Yield could be increased (and employment also) by increasing fishing effort during the next few years, and imposing few regulations. This means reinforcing the present tendency and to manage the fishery on a high-yield basis.

Other sections of the Orinoco River (internal and coastal delta) could be managed differently. They could be maintained at relatively low levels of exploitation in order to conserve the present species composition and the highest diversity of the community. Further growth of the fishery could later be based on these protected areas.

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References

KAPETSKY, L.M. 1974. Growth, mortality and production of five fish species of the Kafue floodplain, Zambia. Ph.D. Dissertation, University of Michigan, Ann. Arbor, MI. 194 p.

NOVOA, D. 1982. Análisis histórico de las Pesquerías del Rio Orinoco, p. 21-50. *In* D. Novoa [ed.] Los Recursos Pesqueros del Rio Orinoco y su Explotación. Editorial Arte, Caracas, 31 p.

NOVOA, D., AND F. RAMOS. 1978. Las Pesquerías Comerciales del Río Orinoco. Corporación Venezolana de Guayana, Caracas.

VÁSQUEZ, E., AND L. SÁNCHEZ. 1984. Variación estacional del plancton en dos sectores del Río Orinoco y una laguna adyacente. Mem. Soc. Cienc. Nat. La Salle XLIV. 121: 11-34.

WELCOMME, R.L. 1976. Some general and theoretical considerations on the fish yield of African Rivers. J. Fish. Biol. 8: 351-364.

1979. Fisheries ecology of floodplain rivers. Longman, London and New York, NY. 371 p.

The Fisheries and Limnology of the Lower Plata Basin

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Abstract

QUIRÓS, R., AND S. CUCH. 1989. The fisheries and limnology of the lower Plata Basin, p. 429–443. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The fish community of the lower Plata River Basin (mainly lower Parana, Uruguay and Plata rivers) is a lightly exploited system with a fishery based mainly on age four to six fishes. Fish catches are related to the Parana River flood regime of preceding years and are regulated by fish movements between the main channel and the floodplain. *Prochilodus platensis* is the most notable species. Analysis of relationships between the fishery structure and the system's ecological characteristics showed the proportion of *Prochilodus* in the catch increased with the increase in importance of the floodplain with respect to the main channel, and with the increase in connections between floodplain waterbodies and main and secondary channels. Zooplankton, benthos and fish biomass are influenced by total nutrient levels and organic matter levels in water and sediments.

Résumé

QUIRÓS, R., AND S. CUCH. 1989. The fisheries and limnology of the lower Plata Basin, p. 429–443. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Les richesses halieutiques du bassin inférieur du Rio de la Plata (il s'agit essentiellement du Parana, de l'Uruguay et du Rio de la Plata, dans leur cours inférieur) sont peu exploitées; on pêche surtout dans ces eaux des poissons de classe d'âge de 4 à 6 ans. Les captures sont liées aux crues du Parana dans les années précédentes et dépendent des déplacements des poissons entre le lit principal et la plaine inondable. *Prochilodus platensis* est l'espèce la plus notable. L'analyse des relations entre la structure des pêches et les caractéristiques écologiques du système a révélé que la proportion de *Prochilodus* capturés s'accroît en fonction de l'importance de la plaine inondable par rapport au lit principal ainsi qu'en fonction de l'augmentation du nombre de voies reliant les plans d'eau de la plaine inondable aux cours d'eau principal et secondaires. La teneur totale des eaux et des sédiments en matières nutritives et en matières organiques influe sur le zooplancton, le benthos et la biomasse des poissons.

Introduction

This paper summarizes ecological features of the lower Plata River Basin and describes the structure of its fishery relative to the flood regime and geomorphology of its tributary, the Parana River. We also summarize studies on fish movements and relate them to fish catches at more than 50 landing sites in the lower Plata Basin. The relationship between flood regime of the Parana River and total fish catches for the lower Basin and subsystems is also presented.

The Plata River Basin drains large parts of Argentina, Uruguay, Paraguay, Brazil, and Bolivia. This paper focuses on its lower part, including the lower reaches of the upper Parana River, the lower Bermejo River and the lower Paraguay, the middle and lower Parana River up to the Plata River, the middle and lower Uruguay and the upper and middle Plata.

The lower Plata River Basin is not a heavily exploited system. Fishery statistics for the lower Plata Basin exist since 1921 with the most important fish landings recorded from 1940. However, the quality of the statistics is poor. The fishery at present is based almost exclusively on fish 4–6 yr old and occasionally older fish. *Prochilodus platensis* is the most notable species and its harvest depends on the demand for industrial processing or export.

The middle Parana ecosystem has been studied intensively by Bonetto and associates (Bonetto et al. 1969b; Bonetto 1975) and by INALI (National Limnology Institute, Santo Tomé, Santa Fé, Argentina). During the last few years there has been renewed interest in these studies as well as in those on fisheries because of several dams that are projected to be built on the middle and upper Parana River. In contrast, the Parana River Delta and the Plata River are the least studied ecosystems in the lower Basin. Yacireta dam is near completion on the Upper Parana and several dams have been constructed on the Parana River and its tributaries in Brazil.

Data Sources and Analytical Methods

Information on total catch by sub-basin and by landing, number of fishermen in each region, and the landing sites was provided by the Dirección Nacional de Pesca Continental (Santa Fé 1548, Piso 7, 1060 Buenos Aires, Argentina). Hydrological information on the Parana, Uruguay and Bermejo rivers was provided by the Dirección Nacional de Construcciones Portuarias y Vías Navegables (Alférez Parejas 100, 1107 Buenos Aires, Argentina). Information on catch per unit effort in the main channel and in island lagoons was taken from a study by the Rosario Station of Instituto Nacional de Investigacion y Desarrollo Pesquero (Paseo de la Ribera y Cordiviola, 2000 Rosario, Argentina) during 1957–58.

Throughout this paper the term "lagoons" means permanent or semipermanent standing waters in the plain, while "island lagoons" means the lagoons on the islands within the river channel. The term "secondary channels" means secondary anabranches of the river flowing into the plain and "secondary streams", including the complex and shifting channels that interconnect them.

Information to compare fish size in the fishery with age of fish in the catch by species came from the following: *Prochilodus platensis* (Cabrera and Candia 1964; Vidal 1967; Cordiviola de Yuan 1971), *Pseudoplatystoma coruscans* (Cordiviola 1966a), *Luciopimelodus pati* (Fortuny and Espinach 1982), *Colossoma mitrei* (Andrade Filho 1985), *Leporinus obtusidens* (Candia unpubl. data), *Salminus maxillosus* (Cordiviola 1966b; Sverlij and Espinach unpubl. data).

Principal component analysis (PCA) and cross-correlation analysis were done according to Davis (1973) and correlation-regression analysis following Draper and Smith (1966). The fishery variables employed in the cross-correlation analysis were: TC (total catch), PC (*Prochilodus* catch) and RC (total catch minus that of *Prochilodus*). The hydrological variables used were: L_{mean} (mean annual hydrological level), L_{min} (monthly mean minimum hydrological level), time integral of hydrological level over the bankfull and time integral under the bankfull (Welcomme 1979). Annual catches are by hydrological year for the Parana River, from September to August. Movement of the time series past one another are expressed by the number of years moved preceded by the minus sign (match position, Davis 1973). Hydrological level corresponds to that at Santa Fe City (19)[1] unless otherwise specified. All regression analyses were also performed with $L_{i,j}$ (monthly mean minimum hydrological level within the years i and j previous to the year of the catch) and $L_{i\text{-}j}$ (monthly mean minimum hydrological level within the period that goes from i to j years previous to the year of the catch). The results are more regular and consistent with minimum hydrological level in each year (L_{min}). The hydrological regime of the middle Parana is such that minimum levels occur in September, at the beginning of spring, and maxima in March–April, at the beginning of autumn. Mean monthly air temperature (TEMP) at several fish landing sites (Servicio Meteorológico Nacional, 25 de Mayo 658, 1002 Buenos Aires, Argentina) was considered as a climatic variable. Information on flooded areas at different flood return periods was provided by Instituto Forestal Nacional (Av. Pueyrredón 2445, 1110 Buenos Aires, Argentina).

Although the fishery as a whole lightly exploits the resource, local fisheries are moderately intensive. Their intensity is also dependent on fishing gear employed. Human population density was low and variable during the period studied. The human population density in the lower Plata River basin during the period 1914–80 (H) was considered as a variable that might be related to the level of effort. Two or more fish species are sometimes grouped together in the commercial catch records. Therefore, a single variable in the principal component analysis represents a "species" group (Table 1).

The total data base is available on request from the authors (see Appendix).

Description of the Lower Plata River Basin

The Plata River System (Fig. 1) is formed by the Parana, Paraguay and Uruguay river basins. With an area of 3.1×10^6 km^2, it is the second largest drainage system in South America after the Amazon River and the fourth largest in the world. The upper Parana River differs markedly in its geomorphological features from the middle and lower Parana River. Its basin shows a stepped and uneven profile; abundant falls and rapids are interspersed with low gradient reaches and extensive floodplains up to the confluence with the Paraguay River. Except for some tributaries originating in the Andes region, the Paraguay River has extensive floodplains with swampy marginal areas; its upper basin is dominated by the "Gran Pantanal", probably the greatest swampy area subject to sheet flooding in South America (Welcomme 1985).

After the confluence with the Paraguay, the hydrological and limnological characteristics of the Parana change to form the middle Parana with its massive floodplain, covering more than 20 000 km^2 (Bonetto et al. 1969b). The lower Parana forms a delta of more than 10 000 km^2. With southeast storm winds tidal effects are felt up to 300 km upstream. No current reversals are registered as far downstream as the delta distributaries which experience reduced flows at high tide only (Urien 1972).

The Uruguay River with its rocky bed resembles the upper Parana. The lower Uruguay widens and deepens considerably before its confluence with the Parana Delta distributaries; its right bank becomes flat and prone to floods.

The Plata River is formed by the junction of the Parana and Uruguay rivers; average discharge is 25 000 m$^3\cdot$ s^{-1} (Urien 1972). The upper river is very shallow and has an average depth of about 1.20 m. Near Colonia City the "principal channel" bifurcates and the main channel crosses the estuary towards La Plata City and continues seaward along the middle of the river (Urien 1972).

At the confluence of the Parana and Paraguay rivers, the latter is higher in suspended matter, nutrients and organic matter (due to the Bermejo River) than the Upper Parana (Table 2). From this point southwards the valley widens. After a stabilization zone, suspended solids tend to decrease and dissolved solids, organic matter and phytoplankton, zooplankton and benthos biomass increase along the length of the river until the beginning of the delta (Bonetto 1976; Drago and Vasallo 1980; Ezcurra de Drago 1980; Jose de Paggi 1980; Perotti de Jorda 1980a).

Sediments in the Parana River Delta distributaries are mostly sand and silts, with mean diameters between 2 and 5 phi grade (Urien 1972). Current velocities in the upper Plata are insufficient for a high sand transport, therefore,

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[1] Numbers in parentheses throughout this paper refer to geographic sites (Fig. 1).

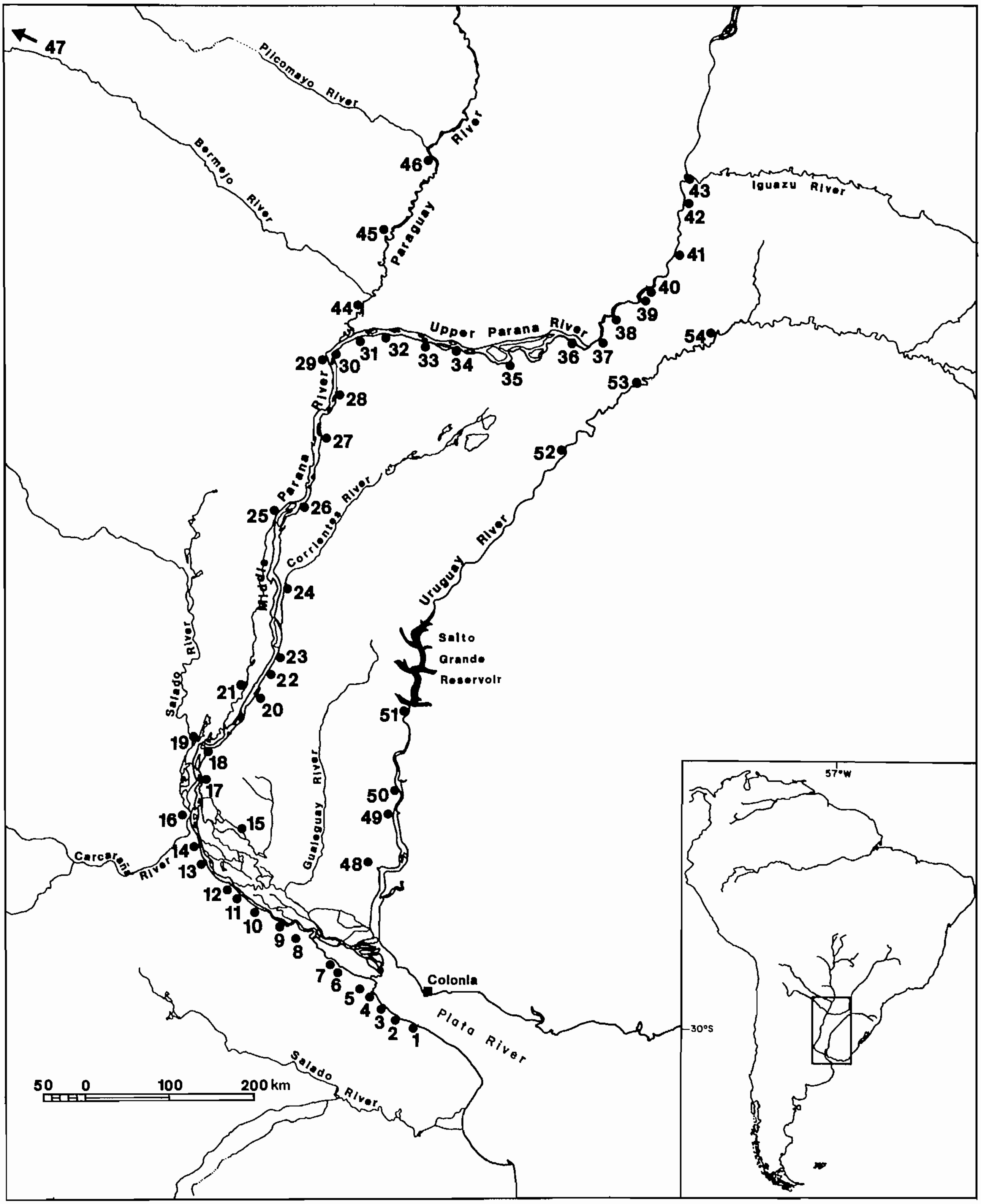

FIG. 1. The lower Plata River Basin. Numbers indicate fish landing sites.

silt and clay comprise the bulk of sediments transported into the Plata River. Silt covers a very extensive area in the upper and middle Plata River. The northern coast is essentially sandy (mean diameters between 1.4 and 2.5 phi grade). On the southern shore sediments are silty sands and clays (3.9 to 7.8 phi grade). The main channel passes against the northern shore where levels of organic matter and nutrients are lower than against the southern bank.

TABLE 1. Fish taxa included in each "species" variable in the principal components analysis.

Fish taxa	Variable
Oxydoras kneri	ARM
Pterodoras granulosus	
Rhinodoras d'orbignyi	
Lycengraulis olidus	ANCH
Parapimelodus valenciennensi	BGTO
Leporinus spp.	BOGA
Pimelodus clarias	BAMAR
Salminus maxillosus	DOR
Ageneiosus spp.	MAND
Sorubim lima	
Paulicea lutkenii	MANG
Pseudopimelodus zungaro	
Pimelodus albicans	MONCH
Luciopimelodus pati	PATI
Megalonema platanum	
Basilichthys bonariensis	PEJ
Brycon orbignyanus	PIRA
Brycon sp.	
Colossoma mitrei	PACU
Prochilodus platensis	SAB
Prochilodus sp.	
Pseudoplatystoma fasciatum	SUR
Pseudoplatystoma coruscans	
Hoplias malabaricus	TAR

Biological Characteristics of the Lower Plata River Basin

In a cross-section of the river, the floodplain is structured such that the density of biotic components increases from the main channel toward the edge of the plain (Table 2). In addition to increases in dissolved solids, biomasses increase for phytoplankton, zooplankton, benthos and fish in the order of: main channel, secondary channels, secondary streams and lagoons. Particularly for fish, banks of the main channel tend to be zones of intermediate biomass between the main channel and secondary streams (Table 2) (Poddubnyi et al. 1981). Fish biomass appears highest in lagoons farthest from the main channel (Cordiviola de Yuan unpubl. data; Quiros and Baigun 1985).

Mean levels of nutrients, total organic matter, and biomass of phytoplankton, zooplankton and benthos of tributaries are generally higher than those of secondary streams (Table 2). Particle size of sediment decreases from the main channel towards floodplain lagoons while organic matter in the water column and sediment increases. As particle size decreases, levels of organic carbon per unit mass of sediment increase (Emiliani 1977; Marchese and Ezcurra de Drago 1983; Copes 1984). Table 2 compares subsystems and is not exhaustive with respect to mean values and variation in time and space. For example, chlorophyll *a* values have been reported at up to 660 mg• m^{-3} in lagoons at the mouth of the Salado River (Bonetto et al. 1969b) with mean values between 9.7 and 12.6 mg• m^{-3} for secondary streams (Perotti de Jorda 1981, 1985). Secondary channels and streams have lower levels of dissolved oxygen and lower pH at high water than does the main channel due to the macrophyte decay cycle in lagoons (Bonetto 1975).

Phytoplanktonic production in the main channel of the middle Parana River does not reach levels attained in the upper Parana and in the Paraguay River north of the Bermejo River mouth (Table 3). In the upper Plata River, levels of chlorophyll *a* and organic matter are higher than in the main channel of the Parana and Uruguay rivers (Quirós and Senone 1985). In addition to phytoplankton biomass, primary production depends on the flood regime, being generally higher at low water. However, net primary production (P) is generally low and since the respiration (R) levels in the water column are relatively high (Perotti de Jorda 1980a) the P/R rate is less than one. In floodplain lagoons production levels (oxygen method) are between 50 and 1 000 mg $C{\bullet}m^{-2}{\bullet}d^{-1}$ (Bonetto et al. 1969b) with an average of 510 mg $C{\bullet}m^{-2}{\bullet}d^{-1}$ as gross production for a whole annual cycle (Perotti de Jorda 1977). The reported net primary production of floating macrophytes varies between 530 and 1 286 mg $C{\bullet}m^{-2}{\bullet}d^{-1}$ of covered surface; values of the same order and magnitude (Table 3) or higher correspond to the "swampy" areas of the floodplain (Neiff 1981).

Although, the contribution of aquatic macrophytes to energy input of the system seems to be far more important than that of the phytoplankton (Table 3), annual production cycles of each are out of phase in the middle Parana River. Macrophyte production follows the thermal regime, with maxima in high falling waters (Lallana 1980; Sabattini unpubl. data). Floating macrophytes particularly *Eichhornia crassipes* can completely cover lagoons. The degree of cover depends on the hydrological cycle, the position and the size of the lagoon within the floodplain. Macrophyte decay could be a key factor in the spatial and temporal organization (Table 2) of biota in the floodplain and in the delta and Plata River.

The major ecological features of the Uruguay River are similar to those of the upper Parana (Bonetto 1975) and follow the same trends as in the main channel of the Parana River. Uruguay River nutrient levels are lower but phytoplankton biomasses are similar (Comisión Técnica Mixta de Salto Grande 1982; Quirós and Cuch 1988).

Structure of the Fishery

The total fish catch from the Parana River for the period 1945–84 was 3 679 $t{\bullet}yr^{-1}$, of which 40% was *Prochilodus*. In the Uruguay and Plata rivers, the catches were 2 560 $t{\bullet}yr^{-1}$ (95% *Prochilodus*) and 4 960 $t{\bullet}yr^{-1}$ (86% *Prochilodus*), respectively. The total catch from the lower Plata River Basin was 11 119 $t{\bullet}yr^{-1}$ of which 73% was *Prochilodus*. Large catches of *Prochilodus* in the Uruguay River came from a single fish landing (Gualeguaychú, 48) in the lower Uruguay. In the middle and upper Uruguay, the catch of *Prochilodus* was proportionally much less. There are also relatively important sport and subsistence fisheries which have not been evaluated.

From Puerto Iguazú (43) to slightly south of the confluence with the Paraguay River, the most common fishing gear is the "espinel" (long-line with numerous fish-hooks), although gill nets are also used. South of the Paraguay confluence the use of long-lines diminishes and the "mallon" (a net panel of stretched mesh of 32 to over 40 cm) and trammel net becomes dominant. Both gears are used in the main channel or in secondary streams; the current drags the fishing gear in places especially prepared for fishing. The "mallon" is used to catch large specimens of *Pseudoplatystoma*

TABLE 2. Phytoplankton, zooplankton, benthos, and fish biomass, bottom sediment, and organic matter in the water column in the lower Plata River Basin.

	Upper Paraná	Paraguay	Middle Paraná	Tributaries	Secondary courses	Lagoons
Phytoplankton[a]						
Chl*a* (mg• m^{-3})	5.8	4.1	6.5 (3.0–8.5)	6.7 (5.4–8.4)	—	8.9 (2.7–91.9)
Biomass (g• m^{-3})	—	—	0.5 (0.1–1.1)	2.3 (1.1–2.6)	1.6 (0.7–5.2)	—
Zooplankton[b]						
Biomass (mg• m^{-3})	—	—	1.4 (0.4–2.6)	—	—	94.0 (8.3–421.6)
Numbers (L^{-1})	1.1	13.0	5.6 (0.7–12.0)	(1.0–23.0)	—	232.0 (11.0–1115.0)
Numbers (L^{-1})	—	—	54.4	151.0	122.3	—
Benthos biomass[c]						
Channel (mg• m^{-2})	0.2	0.7	1.9 (0.0–8.2)	—	—	7180.0
Bank (mg• m^{-2})	—	—	128.1	—	—	—
Channel (mg• m^{-2})	—	—	1.5 (0.01–4.7)	473.0 (0.01–4324.0)	237.0 (0.01–2340.0)	— —
Bottom sediment[d]						
Channel (*phi* grade)	1,2	1,2,3	2,3	2,3,4–4,5,6	2,3,4	7,8
Bank (*phi* grade)	—	2,3,4	2,3,4,5	—	—	—
Organic matter[c] (mg 0_2• L^{-1})	2.6 (1.2–5.9)	9.2 (3.0–16.4)	3.9 (2.4–7.5)	— —	4.4 (2.4–9.2)	5.7 (2.8–27.0)
Organic matter[f] (mg 0_2• L^{-1})	—	—	—	15.0 (6.4–28.8)	—	15.7 (7.7–28.3)
Fish biomass[g]) (kg• L^{-1})	150[h] (50–250)	— —	193[h] (85–370)	—	313[h] (11–1500)	876 (66–6700)

[a] Perotti de Jorda (1980a, b); García de Emiliani (1981, 1985); García de Emiliani and Anselmi de Manavella (1983).

[b] José de Paggi (1980, 1983); Paggi (1980).

[c] Ezcurra de Drago (1980); Marchese and Ezcurra de Drago (1983).

[d] Bertoldi de Pomar (1980, 1984) and unpubl. data. Wentworth scale; *phi* grade 2, medium sand; *phi* grade 8, silty clay.

[c] Maglianesi (1973); Bonetto (1975); permanganate oxidability.

[f] Maglianesi and Depetris (1970), INALI files (Inst. Nac. de Limnología, J. Maciá 1833, 3016 Santo Tomé, Santa Fe, Argentina). Only the Salado River.

[g] Ponds: Bonetto et al. (1969, 1970a, 1970b); Cordiviola de Yuan (1977) and unpubl. data. Main channel: Upper Paraná River, Biosonics Inc. 1985 (4520 Union Bay Place NE, Seattle, Washington 98105), Middle Paraná River and secondary courses; Poddubnyi et al. (1981) (Agua y Energía Eléctrica, Ger. Paraná Medio, Hipólito Irigoyen 2856, Santa Fe, Argentina).

[h] Only for comparisons, we assume: one count, one fish, 1 kg.

spp., *Paulicea lutkenii*, *Salminus maxillosus* and *Brycon orbignyanus* (Cordini 1955). At the latitude of Parana City (18) and up to the start of the delta at Rosario City (13), the trammel net is the most frequently used gear in the main channel; long-lines are also used. The gill-net is used in floodplain lagoons. South of Rosario (13) long-lines are the most common gear in the main channel; trammel nets are also used. On the floodplain (Victoria, 15) gill nets and beach seines are used. In the Plata and lower Uruguay rivers (Gualeguaychú, 48) beach seines are used for industrial fisheries. In the rest of the Plata River long-lines, gill nets and encircling nets are used. In the middle and upper Uruguay River long-lines are used except in Salto Grande Reservoir where gill nets are employed.

Most fishermen use small boats. In the Plata River small craft 10 to 15 m long are used. This type of ship is also used in the Parana, mainly south of Parana City (18), for collecting catches of the individual fishermen (Cordini 1955).

The only information on effort available is the somewhat unreliable estimate of the number of fishermen per month per fish landing for the period 1982–84. For this period 1543 fishermen are reported for the whole system which would give a catch of 22.8 kg• fisherman^{-1}• d^{-1} for the period 1982–84. The information on catch per unit effort per fish landing (considering the full-time fisherman as the unit effort) varies between 3 and 382 kg• fisherman^{-1}• d^{-1} in the Parana River and from 28 to 411 and 2 to 138 kg• fisherman^{-1}• d^{-1} in the Plata and Uruguay rivers, respectively. These differences reflect different types of fishery in different parts of the system and also the low quality of information available. One consistent observation is that the largest catches per unit effort come from fish landings with a greater proportion of *Prochilodus* in the catch (Table 4).

The relationship of catch per unit effort and *Prochilodus* frequency in the catch is also correlated with morphology of the Parana floodplain and the Parana Delta. There seems to be a positive relationship of both variables with the relative size of the floodplain with respect to the channel (floodplain width divided by channel width) and the drainage characteristics of the plain.

The proportion of *Prochilodus* in the catch and catch per unit effort increases with the degree of importance of the floodplain with respect to the main channel, and with the

TABLE 3. Macrophyte and phytoplankton primary production in the lower Plata River Basin (in mg C• m^{-2}• d^{-1}).

	Upper Paraná	Paraguay	Middle Paraná	Lagoons	Swamp
Phytoplankton C^{14} method[a]	240 (7–960)	343 (60–750) 18 (5–61)	31–99[d] (2–285)		
Oxygen method[d] (gross production)			102[e] (1–800)	510[f] (25–1270)	
Macrophyte[c] (net production)				880 (530–1286)	680[g]

[a] Bonetto et al. (1979, 1981, 1983). Without respiration correction.

[b] Perotti de Jorda (1977, 1984).

[c] Poi de Neiff and Neiff (1977); Lallana (1980); Bayo et al. (1981); Sabattini (unpubl. data).

[d] Near confluence with Paraguay River, right and left margin respectively.

[e] At Paraná City.

[f] Only one lagoon.

[g] Aerial production.

TABLE 4. Catch per unit effort in the lower Plata River Basin (1982–84) and frequency of *Prochilodus* in the catch (1972–84). Mean value and range of each variable.

		Middle Paraná				
	Upper Paraná	Up to Hernandarias (20)	Up to Diamante (17)	Up to San Nicolás (11)	Lower Paraná	Plata River
Catch per unit effort (kg• fisherman^{-1}• d^{-1}	18.3 (2.5–64.6)	11.8 (6.6–30.1)	120.9 (66.0–230.1)	133.9 (7.9–381.6)	12.1 (5.5–20.5)	614.5 (109.0–1127.4)
Prochilodus Frequency in the catch	0.23 (0.003–0.54)	0.09 (0.02–0.25)	0.32 (0.22–0.43)	0.45 (0.25–0.95)	0.21 (0.00–0.46)	0.73 (0.56–0.98)

number of connections between floodplain waterbodies and channels. These relationships would operate through accessibility to fish by the fishermen, as well as accessibility to floodplain waterbodies by fish to reach adequate feeding and spawning grounds.

The catch per unit area for the system is 3.5 kg• ha^{-2}• yr^{-1} for the period 1945–84 and 7.5 kg• ha^{-2}• yr^{-1} for the period 1982–84, excluding the Paraguayan upper Parana catch (Bayley 1984). This last value is 25 % or less of the potential estimated for the system using Welcomme's equations (1979, 1986). It is possible that actual catches are at least twice those reported for Argentina, although the fish community as a whole is lightly exploited. The Paraguay River with a floodplain area of 10 500 km^2, produces a yield per maximum flooded area of 11 kg• ha^{-2}• yr^{-1}, about 25 % of Welcomme's lower limit of his 40–60 norm (Bayley, Illinois Natural History Survey, University of Illinois, 607 East Peabody Drive, Champaign, IL 61820, USA, pers. comm.).

To summarize the structure of the fishery in the lower Plata River Basin, we performed a principal component analysis of the catch composition as a function of the fish landings. Results were later related to the type of fishery that was regionally dominant. To make data independent of the effect of effort on total yield we transformed all the "species" variables to catch-frequencies and the analysis was linearly performed according to the variance-covariance matrix (Davis 1973). The first eigenvector (Table 5) explained 63 % of the total variation and weighted *Prochilodus* positively and *Pseudoplatystoma* spp. negatively. The second eigenvector weighted *Pseudoplatystoma* spp. and *Prochilodus* positively and *Pimelodella* spp. and to a lesser extent *Luciopimelodus pati* negatively. In the principal components space three main groups were separated (Fig. 2). Two of them, A and C, represent extreme cases of unspecific fisheries. In the case of A, the fish landing sites were clustered with fishing gears selective for *Pseudoplatystoma* spp., such as hooks and "mallon". These sites are located on the main channel where most of the effort seems to be concentrated. Also, these sites include the middle Parana north of Helvecia City (21) and the upper Parana and Paraguay rivers. In the case of C, two fish landing sites are represented on the middle Plata River, one in the Parana Delta away from the main channel and one in the lower Uruguay, some distance north of the Parana mouth. These are regions of high captures of *Prochilodus* (over 95 %) by an industrial fishery. Fishing gear employed was mainly seines, and some gill nets.

The remaining sites were grouped in B, within which three subgroups can be distinguished. B$_1$ gathered all landing sites of the middle Parana south of Santa Fe Parana (18–19) and landing sites on the upper Parana and upper Uruguay rivers. Catches of *Prochilodus* from these sites varied between 25 and 50 % of the total catch because fishing gear of trammel nets, gill nets and hooks was less selective.

The three remaining fish landing sites of the Plata River, two of them located almost at the mouth of the delta, were

TABLE 5. Eigenvalues, % variance explained, and eigenvectors for species catch frequency PCA.

Species Variable	(Principal Component		
(See Table 1)	1	II	III
ARM	−0.00	−0.11	0.14
ANCH	0.01	−0.02	−0.02
BGTO	0.01	−0.52	−0.18
BOGA	0.03	−0.13	−0.03
BAMAR	0.01	−0.02	−0.01
DOR	0.02	−0.05	−0.05
MAND	0.01	−0.05	0.04
MANG	−0.06	0.03	0.34
MONCH	0.00	−0.02	−0.04
PAT	−0.09	−0.23	−0.46
PEJ	0.02	−0.03	−0.04
PIRA	−0.01	−0.01	0.22
PACU	−0.10	0.13	0.65
SAB	0.77	0.50	−0.19
SUR	−0.62	0.62	−0.31
TAR	0.01	−0.07	−0.05
Eigenvalue	1120.7	332.4	116.6
% variance explained	63.3	18.8	6.6

grouped in B_2. One of them gathers fish from the Delta and from the lower Uruguay River (Tigre, 5), where *Prochilodus* is over 55 % of the total catch. Group B_3 clustered fish landing sites in the lower Parana, the main channel where *Prochilodus* catches were low or nonexistent but those of *Luciopimelodus pati* and *Pimelodella* spp. were high. The rest of B included fish landing sites on the middle Parana with high historical catches of *Prochilodus* (Diamante, 17), and landings on the upper Parana, upper Uruguay and middle Bermejo rivers.

The third axis (Table 5) separated into B and C the fish landings of the middle Parana from those of the upper Parana and upper Uruguay. For those on the upper Parana the proportion of *Colossoma mitrei*, *Paulicea lutkenii* and *Brycon orbignyanus* is higher than in the middle Parana. In the upper Uruguay the proportion of *Brycon orbignyanus* and *Pseudopimelodus zungaro* is larger (Fig. 3). The composition of the catch at present in the three fish landing sites in the region of Rosario (13) agrees with the results of this ordination (Vidal unpubl. data). The composition in five landing sites in the Brazilian Gran Pantanel (Paiva 1984) are distributed in clusters A and B of our principal components space (Fig. 2). Although all catches include *Colossoma* and *Paulicea*, in three of them *Pseudoplatystoma* surpasses 50 %. Studies of catch and effort in the main channel and floodplain show *Colossoma*, *Paulicea* and *Brycon* are available only in late spring and summer at low rising waters and high waters in the middle Parana south of Santa Fe-Parana (18–19) (Anonymous 1958; Oldani and Oliveros 1984).

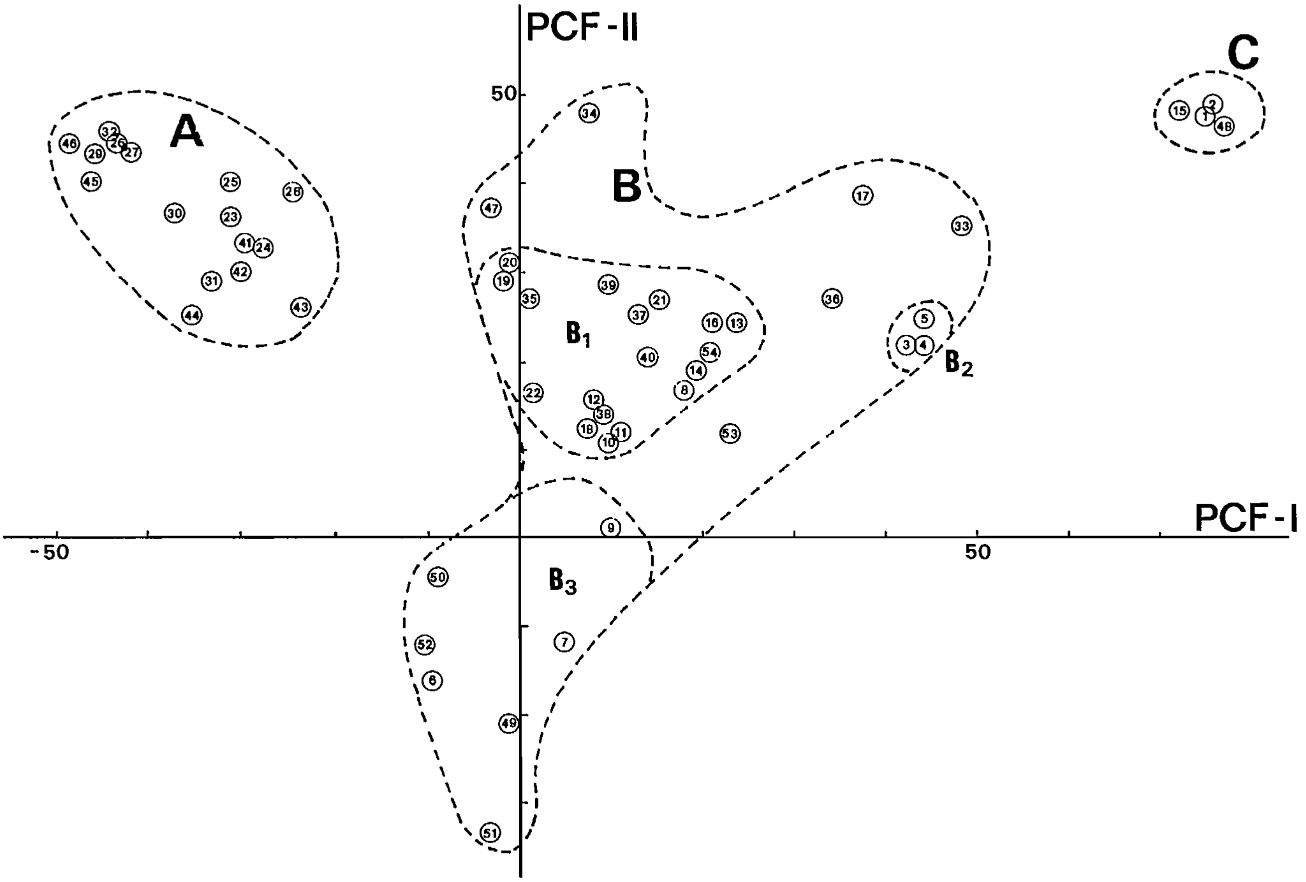

FIG. 2. Position of each fish landing site in the two first axes principal components space.

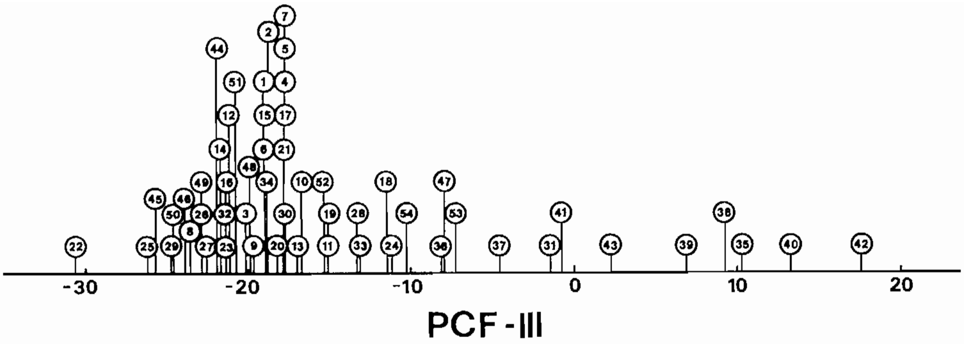

FIG. 3. Position of each landing site in the third principal components axis.

Catch and Flood Regime

Hydrological levels of previous years, especially mean annual (L_{mean}) and monthly mean minima (L_{min}) appear to influence catches in the Parana River (Table 6). This relationship holds for total catch, catch of *Prochilodus*, total catch minus that of *Prochilodus*, and catches of *Pseudoplatystoma* spp., *Salminus maxillosus* and *Luciopimelodus pati*. The relationships are generally better with L_{min} and time integral of water level under bankfull. The relationship between L_{min} and TC increases from one year before the catch, being highest in the years -5, -6 and -7. The relationship with RC follows the same tendency and is highest for years -6 and -7.

The mean L_{min} for years -5, -6 and -7 explains 35 % of the variation in TC, and for the years -6 and -7 explains 47 % of the variation in RC (Table 7).

TABLE 7. Paraná River. Regressions of total catch (TC), total catch minus that of *Prochilodus* (RC), and *Prochilodus* catch (PC) against the monthly mean minimum hydrological level (L) and human population density (H).

N	Regression	R^2	P<
36	TC = 2394 + 763 $L_{5,6,7}$	0.35	0.001
18 (1)	TC = 2181 + 595 $L_{5,6,7}$	0.21	0.03
18 (2)	TC = 3056 + 568 $L_{5,6,7}$	0.29	0.01
36	TC = −78.7 + 608.2 $L_{5,6,7}$ + 0.5 H	0.50	0.001
36	RC = 1423 + 479 $L_{6,7}$	0.47	0.001
36	RC = -83.5 + 417.1 $L_{6,7}$ + 0.31 H	0.61	0.001
36	TC = 1365 + 1625 $L_{1\text{-}9}$	0.57	0.001
36	RC = 914 + 907 $L_{3\text{-}8}$	0.67	0.001
36	PC = 768 + 434 $L_{1\text{-}6}$	0.23	0.005

Data were divided into two periods to assess the influence of effort. In general, for the first period, the explained variance was lower. However, in the one exceptional case of $L_{5,6,7}$ for TC both regression lines do not have significantly different slopes and their intercepts differ by 40 % (Table 7). Human population increase (H) added to the regression explained 50 % and 61 % of the variation in TC and RC, respectively (Table 7). Nevertheless, the increase is smaller if both periods are analyzed separately. If the average L_{min} for the previous years -1 to -9 ($L_{1\text{-}9}$) is considered as the independent variable then 57 and 61 % of the respective variations in TC and RC are explained. In this case the explicative value of (H) becomes non significant. This last fact, together with its low explicative value in each subset taken separately would lead us to reject H as an important explanatory variable. The explicative value of the hydrological levels in the previous years -8 and -9 might be due to the fact that age classes, mainly of the big silurids, are actually taken by the fishery (Oldani and Oliveros 1984). In Table 7, the best explanatory relationships obtained for TC, RC and PC are presented. The low explanatory value of the hydrologic variables on PC would indicate the industrial fishery of *Prochilodus* depends on other factors.

Although the effort applied in open zones by the fishery is relatively high, the great mobility of the fish stocks makes the fishery very sensitive to the management regulation

TABLE 6. Correlation of total catch (TC), total catch minus that of *Prochilodus* (RC), *Prochilodus* catch (PC), *Salminus* catch (DOR), *Pseudoplatystoma* catch (SUR), and *Luciopimelodus* catch (PAT) against monthly mean minimum hydrological level in previous years. Analysis was performed for the total period 1945–81 (T, n=36), first period 1945–63 (1P, n=18), second period 1963–81 (2P, n=18) and match position (Year).

Year	TC			RC			PC			DOR	SUR			PAT		
	T	1P	2P	T	1P	2P	T	1P	2P	T	T	1P	2P	T	1P	2P
0	0.23	−0.18	0.23	0.15	−0.35	0.12	0.25	0.02	0.31	0.11	0.12	−0.34	−0.14	0.18	−0.24	−0.10
−1	0.35	0.22	0.27	0.20	−0.30	0.26	0.41	0.50	0.21	0.10	0.21	−0.04	0.02	0.20	−0.23	0.05
−2	0.37	0.11	0.46	0.27	−0.08	0.37	0.36	0.20	0.45	−0.10	0.34	0.35	0.24	0.22	−0.16	0.24
−3	0.38	−0.17	0.67	0.38	−0.06	0.56	0.27	−0.17	0.63	−0.21	0.39	0.26	0.39	0.28	−0.22	0.49
−4	0.32	−0.05	0.45	0.38	0.07	0.48	0.16	−0.11	0.30	−0.20	0.36	0.36	0.26	0.34	0.07	0.44
−5	0.46	0.33	0.47	0.43	0.30	0.40	0.36	0.20	0.44	0.11	0.35	0.44	0.17	0.43	0.38	0.49
−6	0.50	0.27	0.55	0.62	0.63	0.58	0.22	−0.11	0.40	0.43	0.49	0.43	0.49	0.51	0.66	0.49
−7	0.44	0.39	0.32	0.59	0.57	0.52	0.15	0.09	0.02	0.44	0.38	0.22	0.24	0.49	0.55	0.42
−8	0.26	0.49	0.02	0.37	0.46	0.33	0.06	0.34	−0.33	0.16	0.24	0.25	0.16	0.36	0.40	0.30

implemented, be it locally or regionally. For example, one of the points farthest removed from the regression line with exceptionally high catch corresponds to the hydrological year that follows the closing of the *Prochilodus* processing factories during the period 1970–74.

Age classes in the Parana River fishery coincide with maxima in the correlation coefficients observed in the cross-correlation analysis (Table 6) (Anonymous 1958; Oldani and Oliveros 1984). In the period 1978–79 the fishery took mainly 4–6 yr old fish for most species (Oldani and Oliveros 1984); as well, in 1957–58 mean sizes corresponded to older specimens (Anonymous 1958).

The results of the analysis by "species" coincide with those obtained for total catch (Table 6) with maximum relationships for years -6 and -7. *Prochilodus* is an exception for two reasons: (i) the relationship of its catch with $L_{\min}$ is lower than for TC, RC and the catch of the other considered "species" and (ii) other maxima occur in years following high values of $L_{\min}$. The analysis of each of the 18 yr subsets (Table 7) approximately coincides with those obtained from the whole data base. For the second period a displacement of the maximum correlation coefficient towards zero year is observed. Once again *Prochilodus* is an exception, in the first period the highest "r" corresponds to the year -1 and in the second period it occurs in the years -2 and -3, although with a more even distribution up to the years -5 and -6. This last observation is also reflected in the analysis of the total catch. The catch of *Salminus*, a top predator, is related to $L_{\min}$ as well as to $L_{\min}$ for years -6 and -7.

The analysis of the mean catch time series corresponding to the Uruguay and Plata rivers gives similar results to those observed for the Parana River, but the percentage of variation in their respective TC and RC explained by the hydrological regime of the Parana River is noticeably lower. In the Plata River the highest values for RC are displaced towards the years -7 and -10. In the Uruguay River, the relationship of catch with the flood regime of the Parana River is appreciably higher than with its own (Quirós unpubl. data). In the Bermejo River the maximum correlation between TC and hydrological regime of the Parana River is given in the years -3 and -4 and has no relation at all with its own, coinciding with observations of *Prochilodus* in the Pilcomayo River by Bayley (1973).

The joint analysis of catch in the three big rivers, Parana, Uruguay and Plata, presents a similar pattern with maxima in "*r*" for the years -5 and -6 for TC, RC and PC. Relative maxima appear in the years -1 and -2 for TC and PC with L_{mean} but these disappear for $L_{\min}$ (Fig. 4). This indicates a relationship between the abundance of *Prochilodus* in the system as a whole in the two years following a big flood and the total amount of water in the floodplain, rather than with the amount of water left in the low water season.

In all the cases the inclusion of the period 1982–84 improves the explained variance in the catch (Fig. 5). In this period exceptionally high maximum and minimum hydrological levels in the Parana River coincided with a noticeable increase in the catch of *Prochilodus*.

Information from the catch and effort studies undertaken in the Rosario (13) zone during the hydrological year 1957–58 (Anonymous 1958) indicates that as hydrological level increases, total fish abundance on the floodplain increases and decreases in the main channel (Fig. 6). This pattern is mainly due to the abundance of *Prochilodus*. This result is repeated for the main channel in studies of catch and effort of the commercial fishery undertaken at the lati-

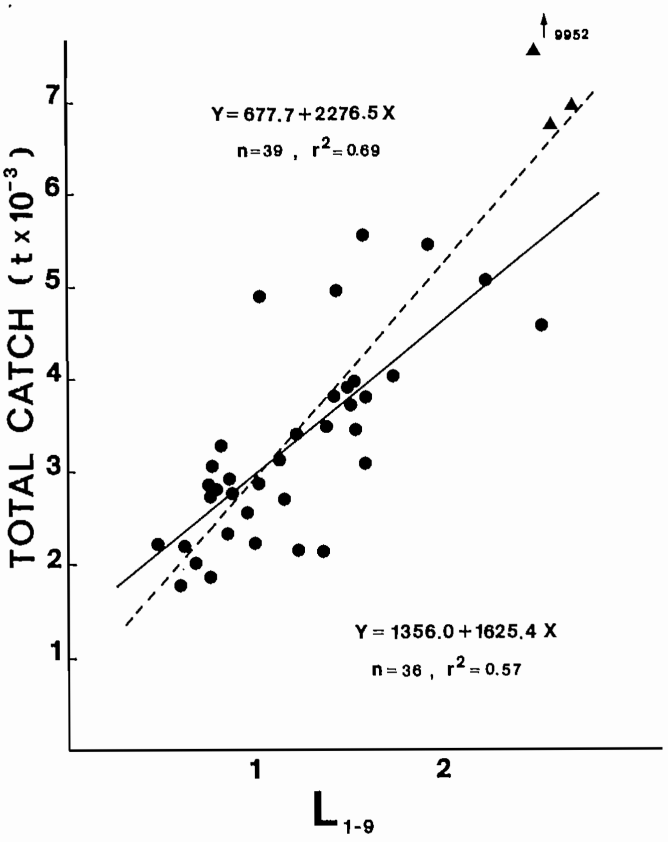

FIG. 4. Time lagged correlation of the mean annual total catch (TC) time series in the Paraná, Uruguay and Plata rivers against the mean annual (●) and monthly mean minimum (▲) hydrological level time series. Time-lagged correlation coefficient versus match position.

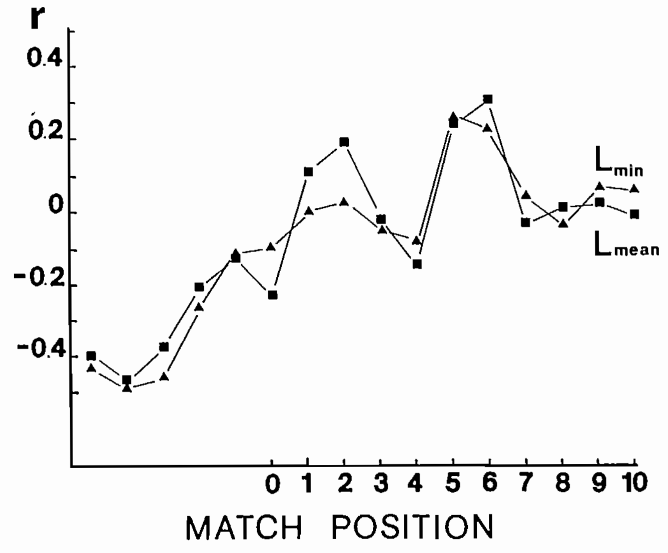

FIG. 5. Paraná River. Regression of total catch (TC) against monthly mean minimum hydrological level within the period that goes from 1 to 9 years previous to the year of the catch (L_{1-9}). (■) years 1945–81, (▲) years 1982–84.

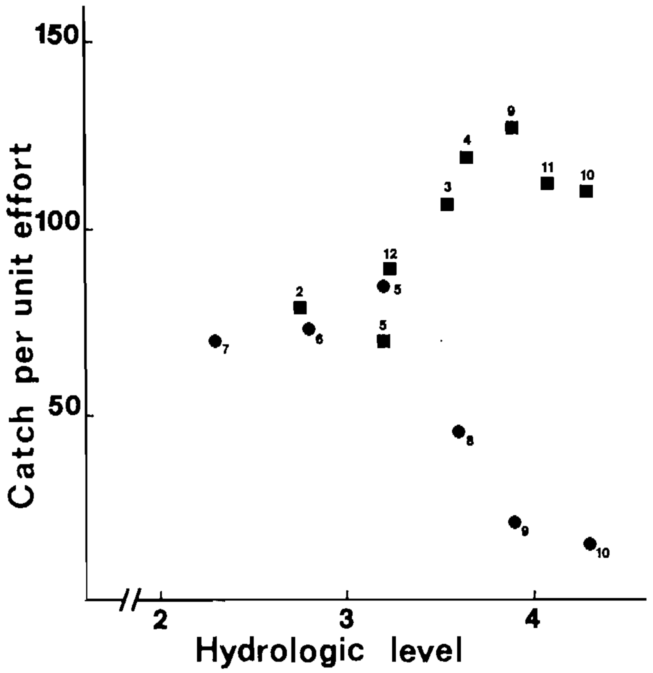

FIG. 6. Paraná River at Rosario (13). Catch per unit effort against monthly mean hydrological level at Rosario (13), 1957-58 hydrological year. (●) main channel catch, (■) floodplain lagoons catch.

tude of Parana City (18) in the period 1967–77 (Oldani and Oliveros 1984) and in studies of experimental fishing during the period 1978–80 (Virasoro unpubl. data). Other species comprise less than 50 % of the catch and do not show such defined behaviour with regard to the floodplain. Their abundance both in the main channel and in the floodplain appears linked to movements along the principal axis of the river (Quirós unpubl. data).

The analysis of commercial catches during the period 1961–81 in the Parana River from the Delta up to the north of the axis Parana-Santa Fe (18–19) gives similar results to those described for catch per unit effort. The distribution of catch of *Prochilodus* at fish landings of the middle and lower Parana follows a similar pattern (Fig. 7); catch maxima are in the periods of falling and low waters and decrease as the hydrological level increases. Minimum catches are obtained during rising high waters and at peak flood. This pattern coincides with the migration pattern reported for *Prochilodus* (Table 8). Tagged fish moved out of the middle Parana in the period of low water and rising low water and returned at falling high water from the Plata River. The catch pattern at all of these fish landings followed that of a fishery on main and secondary channels and not on floodplain lagoons (Fig. 7). Landings in the Parana Delta followed the same pattern almost to the mouth near the Plata River (Tigre, 5). For the rest of the catch, maxima seem to depend on movements of fish along the main axis of the river in response to flood and possibly thermal regimes (Quirós unpubl. data).

Catch patterns for *Prochilodus* in the middle Plata River (Quilmes, 2) are opposite to those for the middle Parana River and its delta (Fig. 8). The catch increases in October but then begins to decline in March (Bonetto 1963; Bonetto and Pignalberi 1964). Its pattern of variation is similar to that for floodplain lagoons (Fig. 6) (Anonymous 1958). The catch north of the mouth of the Parana on the lower Uruguay River (Gualeguaychú, 48) varied like that for the middle Plata River (Quilmes, 2). However, in the Uruguay River the period of high catch may last longer.

TABLE 8. *Prochilodus* frequency recaptured during 6 months after tagging in the Lower Plata River Basin. Upstream (↑) and downstream (↓) main channel migration, upstream, (→) and downstream (←) movement and recapture in the plain, local movement (← →).

Month	Tagging Place	Migration or movement ↑	↓	←	→	← →
1	middle Paraná plain[c]	—	—	0.29	—	0.71
3	middle Paraná plain[b]	—	—	0.24	0.22	0.54
	middle Paraná plain[b]	—	—	1.00	—	—
4	Plata River (2)[a]	1.00	—	—	—	—
5	main channel (27)[a]	0.80	—	—	—	0.20
6	middle Paraná plain[b]	—	0.22	—	0.63	0.15
7	middle Paraná plain[a]	—	0.44	—	0.13	0.43
	middle Paraná plain[a]	—	0.20	—	0.05	0.75
8	middle Paraná plain[a]	—	0.20	—	0.05	0.75
	main channel (18)[c]	0.06	0.47	—	—	0.47
9	middle Paraná plain[a]	—	0.20	—	0.05	0.75
	middle Paraná plain[b]	—	—	0.24	0.22	0.54
	main channel (18)[c]	0.06	0.47	—	—	0.47
	main channel (31)[a]	0.29	0.12	—	—	0.58
10	Plata River (2)[a]	0.60	—	—	—	0.40
11	Plata River (2)[a]	0.60	—	—	—	0.40
12	Middle Paraná plain[b]	—	—	1.00	—	—

[a] Bonetto and Pignalberi (1964).
[b] Bonetto et al. (1971).
[c] Espinach et al. (1982).

Temperature is the principal factor determining the disappearance of big shoals of *Prochilodus* from the Plata River in winter (Bonetto 1963). Catches in the middle Plata River (Quilmes, 2) are positively related with mean monthly air temperature (Fig. 9). However, catches at the mouth of the Parana Delta (Tigre, 5) at a fish landing scarcely 50 km north of Quilmes (2) are negatively related to temperature (Fig. 9). Catches at fish landings of the Parana Delta and the middle Parana correlate negatively with temperature; however, on the lower Uruguay River (Gualeguaychú, 48) catches of *Prochilodus* present a positive relationship with temperature similar to that of middle Plata River. Migrations of *Prochilodus* seem to be linked more to the flood regime of the Parana River, although we cannot reject the effect of temperature.

Changes in catches for the rest of the species in the middle Parana River and its delta seem to be more closely linked to their migrations along the main axis of the river (Quirós unpubl. data). Nevertheless, as in the middle Plata River, they follow similar patterns to those of catches of *Prochilodus*. Catches in the lower (Gualeguaychú, 48) and middle (Colón, 50) Uruguay River do not present a defined relationship with temperature.

Catch and Fish Movements

The results of fish tagging in the lower Plata Basin were analyzed in terms of the principal axis of the river, without attention to fish movements to and from the floodplain. Patterns of recaptures (Bonetto et al. 1971; Bonetto and Pignalberi 1964; Espinach Ros et al. 1982) of *Prochilodus* specimens tagged on the floodplain suggest that *Prochilodus*

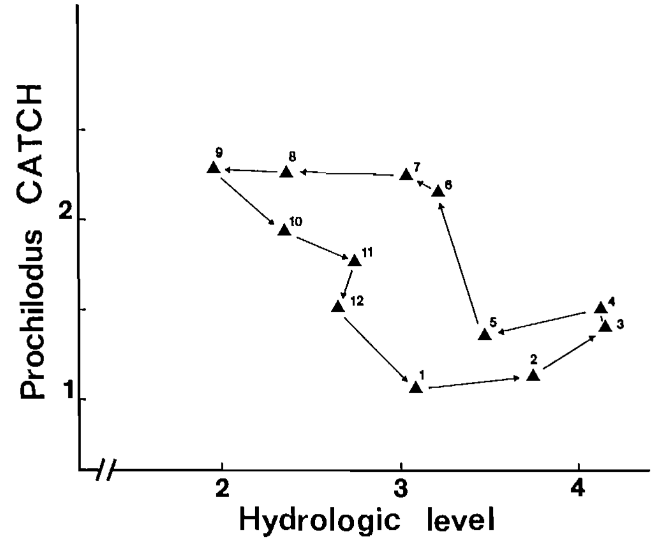

FIG. 7. Paraná River at Puerto Gaboto (16). *Prochilodus* catch (t• 10^{-1}) against monthly mean hydrological level at Santa Fe (19). Numbers indicate month of the year.

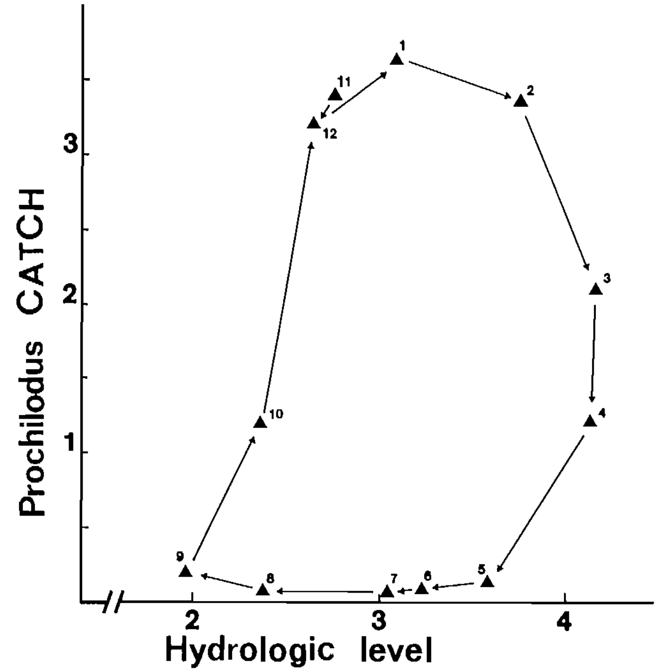

FIG. 8. Plata River at Quilmes (2). *Prochilodus* catch (t• 10^{-2}) against monthly mean hydrological level at Santa Fe (1). Numbers indicate month of the year.

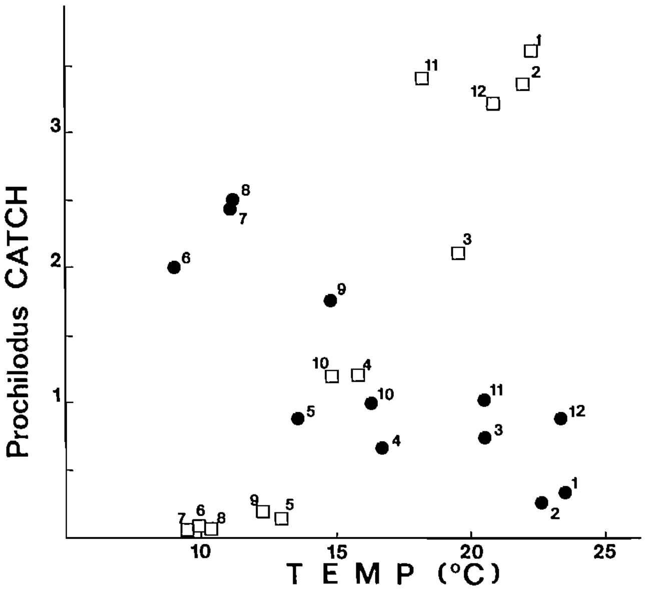

FIG. 9. *Prochilodus* catch against monthly mean air temperature. (□, t• 10^{-2}) Plata River at Quilmes (2). (●, t• 10^{-1}) Paraná River Delta at Tigre (5). Numbers indicate month of the year.

migrates downstream along the main channel only at falling water or low rising water, south of the Santa Fe–Parana (18–19) axis (Table 8) (Poddubnyi et al. 1981). Movements reported as upstream migrations for fish initially caught on the floodplain in lagoons or secondary channels are short movements either along the channel with reentries to the floodplain or along tributaries and secondary channels of the floodplain. A great proportion of tagged *Prochilodus* showed no movement and were recaptured near the tagging site at all stages of the hydrological cycle (Table 8). Recaptures in the channel downstream were made in months of low rising water when fishermen reported fish entering the trammel nets "from above", that is in the direction of the current; at the same time catches increased in the Plata River (Fig. 8).

General Conclusions

The exploitation level of fish in the whole system is low with the lower Plata River Basin fishery fundamentally based on the capture of large specimens of *Prochilodus* and other big migrators. As in other rivers with extensive floodplains (Welcomme 1979, 1985, 1986), catches depend on flooding intensity and on the amount of water remaining in the system during the low water season in the years in which the age classes taken by the fishery were born. As noted earlier, the magnitude of the high water phase affects the size of stocks through improved reproduction, survival and growth of the fish; the minimum water level affects natural survival and ease of capture during the low water phase (Welcomme 1975, 1986; Welcomme and Hagborg 1977). In the middle Parana floodplain, total catches are related both to high and low water phases, but the relationships appear stronger with the latter. Of fish taken by the fishery, *Prochilodus* appears to be the species most directly dependent on the floodplain. *Prochilodus* catches seem to be more directly related to the amount of water remaining in the floodplain in the years immediately preceding the catch and to the strength of low and high water phases 4 or 5 yr previously. A direct effect might be massive mortalities of fish being trapped in drying floodplain pools in the low water season (Bonetto 1975). The remaining species appear to be affected most by flood levels 5–7 yr previous to the catch. Others are affected by the low water phase and at least one does not show any difference in relation to the low and high water phases. For the system as a whole, catch is related to the amount of water both in high and low water phases in years fish were hatched. Moreover catch could also be related to the magnitude of the high water phase in the two preceding years.

Both the catch-per-unit-effort and the proportion of *Prochilodus* in the catch increase towards the Plata River. The relative abundance of *Prochilodus* along the principal axis of the river appears to be inversely related to the proportion of backswamp in the floodplain. In floodplain lagoons and swamps, the proportion of *Prochilodus* is very high and is practically the only migratory species present, with the exception of some young specimens of other species (Bonetto et al. 1969a; Bonetto et al. 1971; Cordiviola de Yuan and Pignalberi 1981).

The temporal structure of the system is fundamentally linked to the flood regime. The influence of the climatic regime seems to be far less important. Phytoplankton production and biomass in the main channel are maximal at low water. In lagoons phytoplankton production and biomass are maximal during the summer but abruptly decrease with the inflow of the sediment laden flood water towards the end of the season (Perotti de Jorda 1977). Macrophyte production in floodplain lagoons starts to increase towards the end of the spring and reaches a maximum in autumn with high waters and then begins its decay (Lallana 1980). In lagoons and shallow marshes towards the end of the spring and beginning of the summer part of the aquatic and interphase vegetation dies producing an enrichment of organic matter. When water starts falling it washes dissolved and particulate organic matter and vegetation debris at different stages of decay towards certain secondary channels, streams and the main channel (Neiff 1978). Floating plant masses can reach the Plata River (Bonetto 1975).

The whole system appears to be spatially structured according to the main axis of the river and follows a second physical axis perpendicular to the first. There appears to be an increase of nutrients, zooplankton, benthos, fish and organic matter (both in the water column and bottom sediments) in the main channel from the upper Parana towards the Plata River. Phytoplankton primary production increases in the same direction in the main channel. From the main channel towards the secondary channels and streams, the mouths of the tributaries and the floodplain lagoons there is an increase in phytoplankton, zooplankton, benthos and fish biomasses as well as in total nutrients and organic matter in the water column and in bottom sediments. Fish biomass in floodplain lagoons appears to increase moving from those most influenced by the main channel to those located in the distal margin of the floodplain. Phytoplankton primary production increases from the main channel toward floodplain lagoons, although net primary production seems to be of little importance compared to that of macrophytes, the importance of which appears to increase towards the distal margin of the floodplain (Bayo et al. 1981). Macrophyte production is the main energy source of the system and its production and decay cycles control the whole secondary production of the system and those of fish in particular (Bonetto 1975; Welcomme 1979; FAO 1980; Bayley 1981; Chapman 1981; Quirós and Baigún 1985).

The spatial structure of the system reinforces previously established relationships between organic matter levels in the water column and fish abundance in the lower Plata Basin (Quirós and Baigún 1985). Both in the main channel and in the floodplain the total biomass of heterotrophs (Table 3) increases in the same direction as total nutrient levels in the water and organic matter in the water and bottom sediments.

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References

ANDRADE FILHO, J.M. DE [ed.]. 1985. Relatorio da segunda Reuniao do Grupo de Trabalho e Treinamento (GTT) sobre Avaliacao de stoques realizada Tamandare. PE (Pernambuco), Julho 1981. Serie Documentos Tecnicos 34, Instituto de Pesquisa e Desenvolvimento Pesqueiro, Brasilia, Brasil: 439 p.

ANONYMOUS. 1958. Rendimiento de pesca en las proximidades de la Estación Hidrobiológica de Rosario. Dirección General de Pesca y Conservación de la Fauna, Buenos Aires, Argentina: 212 p. (typed).

BAYLEY, P.B. 1973. Studies on the migratory characin, *Prochilodus platensis* Holmberg 1889 (Pisces, Characoidei) in the River Pilcomayo, South America. J. Fish Biol. 5: 25–40.

1981. Fish yield from the Amazon in Brazil: comparisons with African river yields and management possibilities. Trans. Am. Fish. Soc. 110: 351–359.

1984. Aquatic environments and fisheries in Paraguay. Report to International Institute for Environment and Development and USAID, Paraguay, 17 p.

BAYO, V., V.H. LALLANA, E. LORENZATTI, AND M.C. MARTA. 1981. Evaluación cuantitativa de la vegetación acuática de las islas del valle aluvial del río Paraná medio. Parte I. Ecología (Buenos Aires) 6: 67–72.

BERTOLDI DE POMAR, H. 1980. Compaña Limnológica "Keratella I" en el río Paraná medio: Sedimentos de fondo. Ecología (Buenos Aires) 4: 31–43.

1984. Estudios limnológicos en una sección transversal del tramo medio del río Paraná. V. Caracteres texturales de los sedimentos de fondo. Rev. Asoc. Cienc. Nat. Litoral 15: 57–78.

BONETTO, A.A. 1963. Investigaciones sobre migraciones de peces en los ríos de la cuenca del Plata. Ciencia e Investigación (Buenos Aires) 19: 12–26.

1975. Hydrologic regime of the Paraná River and its influence on ecosystems. Ecol. Stud. 10: 175–197.

1976. Calidad de las aguas del río Paraná. Introducción a su estudio ecológico. Dirección Nacional de Construcciones Portuarias y Vías Navegables, Buenos Aires, Argentina. 202 p.

BONETTO, A.A., M. CANON VERON, AND D. ROLDAN. 1981. Nuevos aportes al conocimiento de las migraciones de peces en el río Paraná. Ecosur 8: 29–40.

BONETTO, A.A., E. CORDIVIOLA DE YUAN, AND C. PIGNALBERI. 1970a. Nuevos datos sobre poblaciones de peces en ambientes leníticos permanentes del Paraná Medio. Physis (Buenos Aires) 30: 141–154.

BONETTO, A.A., E. CORDIVIOLA DE YUAN, C. PIGNALBERI, AND O. OLIVEROS. 1969a. Ciclos hidrológicos del río Paraná y las poblaciones de peces contenidas en las cuencas temporarias de su valle de inundación. Physis (Buenos Aires) 29: 213–224.

1970b. Nuevos aportes al conocimiento de las poblaciones ícticas en cuencas temporarias del valle de inundación del Paraná Medio. Acta Zoológica Lilloana 27: 135–153.

BONETTO, A.A., W. DIONI, AND C. PIGNALBERI. 1969b. Limnological investigations on biotic communities in the Middle Parana River Valley. Verh. Internat. Verein. Limnol. 17: 1035–1050.

Bonetto, A.A., and C. Pignalberi. 1964. Nuevos aportes al conocimiento de las migraciones de peces en los ríos mesopotámicos de la República Argentina. Comunicaciones del Instituto Nacional de Limnología 1, Santo Tomé, Santa Fé, Argentina. 19 p.

Bonetto, A.A., C. Pignalberi, E. Cordiviola De Yuan, and O. Oliveros. 1971. Informaciones complementarias sobre migraciones de peces en la cuenca del Plata. Physis (Buenos Aires) 30: 305–320.

Bonetto, C.A., A.A. Bonetto, and Y. Zalocar. 1981. Contribución al conocimiento limnológico del río Paraguay en su tramo inferior. Ecosur 8: 55–88.

Bonetto, C.A., Y. Zalocar, P.M. Caro, and E.R. Vallejos. 1979. Producción primaria del fitoplancton del río Paraná en el área de su confluencia con el rio Paraguay. Ecosur 6: 207–227.

Bonetto, C.A., Y. Zalocar De Domitrovic, and E.R. Vallejos. 1983. Fitoplancton y producción primaria del río Alto Paraná (Argentina). Physis (Buenos Aires) 41: 81–93.

Cabrera, S.E., and C. Candia. 1964. Contribución al conocimiento de la biología del sábalo (*Prochilodus platensis*) del Río de la Plata. Revista de Investigaciones Agropecuarias (Buenos Aires) 1: 57–83.

Chapman, D.W. 1981. Practical fisheries assessment in a tropical floodplain. Fisheries (Bethesda) 6: 2–6.

Comisión Tecnica mixta de salto grande. 1982. Evaluación de los resultados de la aplicación del Programa de Calidad de Aguas en el período julio 1976–abril 1981. Comisión Técnica de Salto Grande, Salto Grande, Argentina–Uruguay. 128 p.

Copes, C.D. 1984. Estudios limnológicos en una sección transversal del tramo medio del río Paraná. VIII: Carbono orgánico en los sedimentos de fondo Rev. Asoc. Cienc. Nat. Litoral 15: 109–115.

Cordini, J.M. 1955. Río Paraná. Sus peces más comunes. Pesca Comercial. Publicación Mescelánea 410. Ministerio de Agricultura, Buenos Aires, Argentina. 86 p.

Cordiviola, E. 1966a. Nuevos aportes al conocimiento de la biología pesquera del "surubí" (*Pseudoplatystoma coruscans*) en el Paraná medio (Pisces, Siluriformes). Physis (Buenos Aires) 26: 237–244.

1966b. Edad y crecimiento del "dorado" (*Salminus maxillosus* Cuv. y Val.) en el Paraná medio. Physis (Buenos Aires) 26: 293–311.

Cordiviola De Yuan, E. 1971. Crecimiento de peces del Paraná medio. I: "Sábalo" (*Prochilodus platensis* Holmberg). Physis (Buenos Aires) 30: 483–504.

1977. Poblaciones de peces del río Paraná. IV: Fluctuaciones de la composición íctica de la laguna "Los Matadores" (Isla Clucellas), Santa Fé. Neotrópica (La Plata) 23: 17–26.

Cordiviola De Yuan, E., and C. Pignalberi. 1981. Fish populations in the Parana River. 2. Santa Fé and Corrientes areas. Hydrobiologia 77: 261–272.

Davis J.C. 1973. Statistics and data analysis in Geology. John Wiley and Sons, New York, NY. 550 p.

Drago, E.C., and M. Vasallo. 1980. Campana limnológica "Keratella I" en el río Paraná medio: características físicas y químicas del rio y ambientes leníticos asociados. Ecología (Buenos Aires) 4: 45–54.

Draper, H., and H. Smith. 1966. Applied regression analysis. John Wiley and Sons, New York, NY., USA.

Emiliani, F. 1977. Fluctuaciones estacionales de las poblaciones bacterianas en el ecosistema: Río Correntoso-Laguna Los Matadores (Santa Fé, Argentina). Revista de la Facultad de Agronomía y Veterinaria (Esperanza, Santa Fé) 1: 73–94.

Espinach Ros, A., A. Fortuny, and M. Arguello. 1982. Resultados preliminares de muestreo y marcación de peces en el area de influencia de la futura represa de Paraná Medio. Informe Técnico 45, código 710. Agua y Energía Eléctrica. Gerenica de Estudios y Proyectos Paraná Medio, Santa Fé, Argentina: 4 p. + tables.

Ezcurra De Drago, I. 1980. Campana limnológica "Keratella I" en río Paraná medio: complejo bentónico del rio y ambientes leníticos asociados. Ecología (Buenos Aires) 4: 89–101.

FAO (Food and Agriculture Organization of the United Nations). 1980. Comparative studies of freshwater fisheries. FAO Fisheries Technical Paper 198.

Fortuny, A., and A. Espinach Ros. 1982. Edad y crecimiento del patí, *Luciopimelodus pati* (Valenciennes 1840), en el Río de la Plata. Ecología (Buenos Aires) 7: 85–94.

García De Emiliani, M.O. 1981. Fitoplancton de los principales cauces y tributarios del valle aluvial del río Paraná: tramo Goya-Diamante. Rev. Asoc. Cienc. Nat. Litoral 12: 112–125.

1985. Fitoplancton de los principales cauces y tributarios del valle aluvial del río Paraná: tramo Goya-Diamante (III nota). Rev. Asoc. Cienc. Nat. Litoral 16: 95–112.

Garcia De Emiliani, M.O., and M.I. Anselmi De Monavella. 1983. Fitoplancton de los principales cauces y tributarios del valle aluvial del río Paraná: tramo Goya-Diamante (II). Rev. Asoc. Cienc. Nat. Litoral 14: 217–237.

Jose De Paggi, S.B. 1980. Campaña limnológica "Keratella I" en el río Paraná medio: zooplancton de ambientes lóticos. Ecología (Buenos Aires) 4: 69–75.

1983. Estudio sinóptico del zooplancton de los principales cauces y tributarios del valle aluvial del río Paraná: tramo Goya-Diamante (I parte). Rev. Asoc. Cienc. Nat. Litoral. 14: 163–178.

Lallana, V.H. 1980. Productividad de *Eichhornia crassipes* (Mart.) Solms. en una laguna isleña de la cuenca del rió Paraná medio. II. Biomasa y dinámica de población. Ecología (Buenos Aires) 5: 1–16.

Maglianesi, R.E. 1973. Principales características químicas y físicas de las aguas del Alto Paraná y Paraguay Inferior. Physis (Buenos Aires) 32: 185–197.

Maglianesi, R.E., and P.J. Depetris. 1970. Características químicas de las aguas del Río Salado Inferior (Santa Fé, Argentina) Physis (Buenos Aires) 30: 19–32.

Marchese, M.R, and I. Ezcurra De Drago. 1983. Zoobentos de los principales tributarios del río Paraná medio en el tramo Goya-Diamate. Su relación con el cauce principal y cauces secundarios. Rev. Asoc. Cienc. Nat. Litoral 14: 95–109.

Neiff, J.J. 1978. Fluctuaciones de la vegetación acuática en ambientes del valle de inundación del Paraná medio. Physis B (Buenos Aires) 38: 41–53.

1981. Panorama ecológico de los cuerpos de agua del mordeste argentino. *In* VI Jornadas Argentinas de Zoología. La Plata, Argentina, Symposia. 236 p.

Oldani, N.O., and O.B. Oliveros. 1984. Estudios limnológicos en una sección transversal del tramo medio del río Paraná. XII: Dinámica temporal de peces de importan económica. Rev. Asoc. Cienc. Nat. Litoral 15: 175–183.

Paggi, J.C. 1980. Campaña limnológica "Keratella I" en el río Paraná medio: Zooplancton de ambientes leníticos. Ecolgía (Buenos Aires) 4: 77–88.

Paiva, M.P. 1984. Aproveitamento de recursos faunísticos do Pantanal de Matto Grosso: pesquisas necessárias e desenvolvimento de sistemas deproducao mais adequados a regiao. Emprese Brasileira de Pesquisa Agropecuaria (EMBRAPA). Documentos 7. Brasilia, Brasil. 71 p.

Perotti De Jorda, N.M. 1977. Pigmentos y producción primaria en el Paraná medio: laguna "Los Matadores" (Santa Fé, Argentina). Physis (Buenos Aires) 36: 89–113.

1980a. Campaña limnológica "Keratella I" enel río Paraná medio: Pigmentos y productividad primaria en ambientes lóticos. Ecología (Buenos Aires) 4: 55–61.

1980b. Campaña limnológica "Keratella I" en el río Paraná medio: Pigmentos y productividad primaria en ambientes leníticos. Ecología (Buenos Aires) 4: 63–68.

1981. Fitoplancton del río Paraná medio (Santa Fé, Argentina). Su variación en relación a factores ambientales en algunos cauces secundarios. Ecología (Buenos Aires) 6: 79–84.

1984. Estudios limnológicos en una sección transversal del tramo medio del río Paraná. IX: Biomasa y productividad del fitoplancton. Rev. Asoc. Cienc. Nat. Litoral. 15: 117–133.

1985. Pigmentos del fitoplancton de ambientes lóticos del valle aluvial del Paraná (tramo Goya-Diamante). Physis B (Buenos Aires) 43: 23–29.

PODDUBNYI, A.G., A. ESPINACH ROS, AND O. OLDANI. 1981. Recursos ícticos del Paraná medio en relación con la construcción de obras hidráulicas (Memorias y recomendaciones). Informe Técnico 33, código 710. Agua y Energía Eléctrica, Gerencia de Estudios y Proyectos Paraná Medio, Sante Fé, Argentina, 105 p.

POI DE NEIFF, A., AND J.J. NEIFF. 1977. El pleuston de *Pistia stratiotes* de la laguna Barranqueras (Chaco, Argentina). Ecosur 4: 69–101.

QUIRÓS, R., AND C. BAIGÚN. 1985. Fish abundance related to organic matter in the Plata River Basin, South America. Trans. Am. Fish. Soc. 114: 377–387.

QUIRÓS, R., AND S. CUCH. 1988. Características limnológicas del embalse de Salto Grande. II: Distribución ydinámica de nutrientes. Ecología (Buenos Aires) 8. (in press)

QUIRÓS, R., AND H. SENONE. 1985. Niveles de nutrientes y pigmentos fotosintéticos en el Río de la Plata interior (55- 59 W- 34-36 S). Serie Informes Técnicos del Departamento de Aguas Continentales 1, Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina. 37 p.

URIEN, C.M. 1972. Rio de la Plata Estuary environments. The Geological Soc. of America, Inc. Memoir 133: 213–234.

VIDAL, J.C. 1967. Contribución al estudio biológico del sábalo de los ríos Paraná y Uruguay. *Prochilodus platensis* (Holmberg) Dirección General de Pesca Y Conservación de la Fauna, Buenos Aires, Argentina. 51 p.

WELCOMME, R.L. 1979. Fisheries ecology of floodplain rivers. Longman, New York, NY.

1985. River fisheries. FAO Fish. Tech. Pap. 330 p.

1986. Considerations of fish yield in rivers. (in press)

WELCOMME, R.L., AND D. HAGBORG. 1977. Towards a model of a floodplain fish population and its fishery. Environ. Biol. Fish. 2: 7–24.

Appendix. Catch frequencies by species and landing sites in the lower Plata Basin.

		ARM	ANCH	BGTO	BOGA	BAMAR	DOR	MAND	MANG	MONCH	PAT	PEJ	PIRA	PACU	SAB	SUR	TAR	TOTAL
1.	Cambaceres	–	–	0.03	0.00	–	0.58	–	–	0.00	1.67	0.64	–	–	97.07	0.00	–	733.27
2.	Quilmes	–	–	0.01	0.02	–	0.44	–	–	–	0.94	0.59	–	–	97.95	0.05	0.00	1707.47
3.	Boca — Riachuelo	–	0.01	0.65	5.87	–	3.00	–	–	–	18.29	15.81	–	–	56.38	0.00	–	261.58
4.	San Fernando	0.15	5.87	5.49	7.20	0.11	7.42	–	–	–	10.42	3.84	–	–	57.31	0.37	1.82	149.63
5.	Tigre	0.01	6.86	1.01	8.57	–	3.83	–	–	–	11.11	5.01	–	–	58.52	1.55	3.36	136.82
6.	Campana	19.64	–	29.15	5.26	–	0.81	2.83	–	–	26.32	2.23	–	–	–	12.75	1.01	4.94
7.	Zarate	6.56	10.71	36.38	2.24	1.10	1.33	–	–	0.16	14.15	5.91	–	0.03	13.27	7.79	0.36	30.81
8.	Baradero	0.52	0.05	20.71	0.26	–	4.63	0.01	–	–	13.47	1.20	–	–	39.59	18.78	0.78	19.22
9.	San Pedro	0.34	10.14	15.08	7.60	–	7.86	0.27	–	–	19.96	2.64	–	–	20.92	8.44	6.75	99.68
10.	Ramallo	6.05	0.03	3.28	5.31	10.80	0.61	1.41	–	13.38	16.90	1.23	–	–	23.49	12.09	5.41	97.81
11.	San Nicolás	9.67	–	1.01	11.71	2.70	2.52	–	–	13.55	14.64	3.93	–	–	24.70	11.65	3.93	72.60
12.	Vá. Constitución	3.47	0.15	2.30	8.51	9.19	0.80	0.52	–	1.49	22.12	0.40	–	0.05	26.46	17.77	6.76	261.67
13.	Rosario	9.97	0.65	1.62	10.37	1.33	4.22	0.18	–	2.69	11.31	0.06	–	0.10	42.75	14.64	0.10	478.18
14.	San Lorenzo	1.72	–	14.44	10.98	–	–	–	–	0.64	12.89	0.02	–	0.08	39.72	18.06	1.45	542.46
15.	Victoria	–	–	1.36	–	0.03	0.35	–	–	–	0.37	0.12	–	0.00	95.27	2.50	–	508.19
16.	Gaboto	2.03	–	8.30	7.21	1.04	3.01	0.01	–	2.56	12.81	0.39	–	0.10	43.07	18.22	1.35	488.92
17.	Diamante	3.43	–	–	2.44	3.15	0.01	1.87	0.04	3.31	5.95	0.67	–	1.43	61.73	15.97	–	163.88
18.	Paraná	15.82	–	2.37	6.62	11.68	0.25	3.35	–	12.02	11.24	–	–	0.97	21.62	14.06	–	166.77
19.	Santa Fé Coronda	0.09	–	0.01	0.47	2.75	0.05	1.09	–	10.46	16.43	–	–	11.44	25.62	31.59	–	161.12
20.	Hernandarias	–	–	–	–	–	–	–	–	1.79	23.49	–	–	12.75	29.08	32.89	–	4.47
21.	Helvecia	2.51	–	–	6.17	1.16	4.60	–	–	7.57	15.24	0.08	–	4.88	37.21	20.33	0.15	296.47
22.	Santa Elena	–	–	–	–	0.33	4.91	–	–	4.17	41.46	–	0.16	1.14	24.78	22.73	–	12.23
23.	La Paz	–	–	–	–	–	1.55	–	–	0.90	20.53	–	–	11.58	8.68	56.76	–	28.93
24.	Esquina	1.90	–	0.22	0.02	–	–	0.28	–	0.67	18.11	–	0.02	21.08	8.55	49.14	–	17.89
25.	Reconquista	–	–	–	–	–	3.94	0.06	–	3.88	15.75	–	–	4.05	10.74	61.58	–	34.80
26.	Goya	0.60	–	–	–	–	–	0.01	0.02	0.36	13.60	–	–	8.87	4.13	72.40	–	8.23
27.	Bella Vista	2.14	0.34	0.17	0.28	0.20	0.21	–	1.95	0.08	11.46	0.28	–	7.60	4.59	70.70	–	107.04
28.	Empedrado	–	–	–	4.24	–	–	–	14.05	–	7.12	–	–	7.29	13.52	53.77	–	63.47
29.	Barranqueras	0.01	–	–	0.27	–	–	0.01	3.88	0.52	14.23	–	–	5.89	1.51	73.69	0.51	153.23
30.	Corrientes	6.90	–	1.31	0.65	–	0.00	0.21	5.95	1.35	10.10	–	0.08	6.99	3.70	62.75	–	156.05
31.	Po. de la Patria	–	–	–	–	–	–	–	23.82	–	12.43	–	–	16.59	–	47.15	–	36.52
32.	Itatí	–	–	–	–	–	–	–	0.39	–	11.63	–	–	11.24	3.49	73.26	–	2.58
33.	Yahapé	–	–	4.07	0.45	–	0.23	–	3.39	–	8.60	–	–	7.92	69.46	5.88	–	4.42
34.	Ita Ibaté	1.20	–	–	–	–	–	–	–	–	3.41	–	–	7.13	45.22	43.05	–	4.24
35.	Ituzaingó	5.22	–	–	–	–	–	2.17	–	–	9.13	–	–	37.83	24.35	21.30	–	2.30
36.	Posadas	8.44	–	8.44	–	–	–	0.41	1.93	–	5.62	–	3.34	9.14	53.66	9.02	–	17.07
37.	Santa Ana	6.03	–	3.90	4.45	1.02	1.07	2.91	3.83	–	3.16	–	17.22	5.78	33.57	19.28	–	20.51
38.	Pto. Maní	14.88	–	1.78	2.05	1.25	0.04	1.06	29.27	–	5.67	–	3.71	9.50	22.44	8.76	–	2.16
39.	Pto. Mineral	13.64	–	2.65	–	–	–	–	–	–	1.14	–	4.55	26.14	31.82	20.08	–	2.64
40.	L.G. San Martín	6.69	–	4.67	3.59	0.78	1.32	0.90	9.50	0.22	1.98	–	7.42	22.81	30.38	9.93	–	14.89
41.	El Dorado	5.02	–	2.51	–	0.04	–	0.04	14.48	–	1.66	–	4.39	17.97	4.75	49.13	–	22.31
42.	Pto. Libertad	–	–	–	–	–	–	–	10.34	–	–	–	10.34	37.93	–	41.38	–	0.58
43.	Pto. Iguazú	1.85	–	4.32	–	–	–	0.12	12.95	–	3.08	–	17.26	14.80	4.93	40.69	0.25	1.62
44.	Bermejo	0.04	–	–	–	–	–	–	11.33	–	31.54	–	–	7.11	–	49.98	–	4.50
45.	Formoso	5.05	–	0.07	1.16	–	–	–	0.75	0.27	15.77	–	0.34	4.57	0.27	71.74	–	14.65
46.	Pilcomayo-Bouvier	–	–	–	–	–	–	–	4.36	–	13.43	–	–	6.79	–	75.42	–	44.02
47.	Río Bermejo	–	–	–	–	–	–	–	20.65	–	6.40	–	–	7.35	28.40	37.19	–	214.38
48.	Gualeguaychú	–	–	5.91	0.00	–	0.02	–	–	–	0.14	0.04	–	–	99.69	0.06	0.00	2249.71
49.	Concep. del Uruguay	–	–	34.70	0.68	–	7.53	1.37	–	–	27.17	2.28	–	–	4.57	4.57	16.44	4.38
50.	Colón	–	–	33.07	5.47	–	2.02	–	–	–	20.60	3.85	2.25	–	8.45	22.89	1.40	101.43
51.	Concordia	5.10	–	56.86	6.27	–	0.39	3.14	0.39	0.39	21.57	1.96	0.39	–	–	3.53	–	2.55
52.	Santo Tomé	13.51	–	27.56	16.21	–	2.16	5.94	1.62	–	16.75	–	0.54	–	0.03	15.67	–	1.85
53.	San Javier	–	–	12.75	11.41	–	2.01	17.45	2.01	–	–	–	12.08	–	34.90	6.71	0.67	1.49
54.	El Soberbio	3.09	–	3.09	17.53	–	8.25	12.37	1.03	–	–	–	4.12	–	37.11	13.40	–	0.97

The Management Problems and Fisheries of Three Major British Rivers: the Thames, Trent and Wye

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Abstract

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River management in England and Wales is the concern of 10 Regional Water Authorities. Water supply, sewage disposal and land drainage requirements demand greatest priority and less than 2% of R.W.A. annual expenditure is directed to fisheries. However, through improved sewage treatment and strict pollution control legislation, parts of the Trent catchment and lower Thames that were once devoid of fish are now recovering. The return of fish communities has been through natural immigration, except for Thames Atlantic salmon (*Salmo salar*) which has been restocked from hatcheries. Direct management of coarse (non-salmonid) fish populations is confined largely to tributaries. Few data exist on coarse fish movement and habitat requirements in the main river, chiefly because sampling difficulties have inhibited the necessary research. More information is available for salmon, and catch statistics from the Wye, plus scale-reading data, have shown changes in the age-composition of stocks. Overexploitation of multi-sea winter fish, or an increased proportion of grilse through changes in Arctic sea temperatures, may explain this trend.

Résumé

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En Angleterre et au pays de Galles, la gestion des cours d'eau relève de 10 services régionaux des eaux. Les besoins en matière d'alimentation en eau, d'évacuation des eaux d'égout et de drainage des terres sont en tête de liste des priorités; par contre, moins de 2% du budget annuel de ces services est consacré aux pêches. Toutefois, des parties du bassin hydrologique de la Trent et du bassin inférieur de la Tamise, autrefois abandonnées des poissons, se rétablissent suite à l'amélioration du traitement des eaux d'égout et d'une lutte rigoureuse contre la pollution des eaux. Le rétablissement des communautés de poissons s'est effectué par immigration naturelle sauf dans le cas du saumon de l'Atlantique de la Tamise (*Salmo salar*) dont les stocks ont été reconstitués par repeuplement artificiel. La gestion directe des populations de poissons communs (autres que les salmonidés) porte principalement sur les tributaires. Il existe peu de données sur les déplacements et les besoins en matière d'habitat des poissons communs dans le cours principal, surtout à cause de problèmes d'échantillonnage qui ont entravé la recherche nécessaire. On dispose d'un plus grand nombre de données sur le saumon; les statistiques sur les prises dans la rivière Wye et des données scalimétriques ont révélé des variations dans la composition selon l'âge des stocks. La surexploitation des saumons pluribermarins ou une plus grande proportion de madeleineaux suite à des variations des températures de la mer dans l'Arctique peuvent expliquer cette tendance.

Introduction

The demands on the resources of river ecosystems are varied and often conflicting. However, economic considerations are paramount and the requirements for water supply, land irrigation and drainage, and sewage disposal are given a higher priority than those of fishery and conservation interests. Different rivers often pose different management problems and for this paper I have chosen three rivers in England and Wales that suffer many of the stresses encountered in British rivers. The characteristics of the rivers Thames, Trent and Wye (Fig. 1, Table 1) are derived from the geological and climatic features of their catchments, on which have been imposed historical and modern exploitations by man.

Both the Thames and Trent were navigable in Roman times and they provided focal points for the development of towns and villages. Their freshwater fish, including the Atlantic salmon, *Salmo salar* L., and eel, *Anguilla anguilla* (L.), provided a valuable food source. As early as the thirteenth century fishery problems were apparent in the Thames, and the Magna Charta of 1215 included the requirement that all weirs belonging to the king should be removed to allow migratory fish to pass upstream. In 1389 an edict was made to prohibit the use of fine-meshed nets to catch juvenile salmon and other species. The increased sophistication of fishing expertise is revealed by another act, introduced in the early seventeenth century, which named fifteen types of net or trap. Although the penalties were severe, such fishing restrictions were often ignored and, by

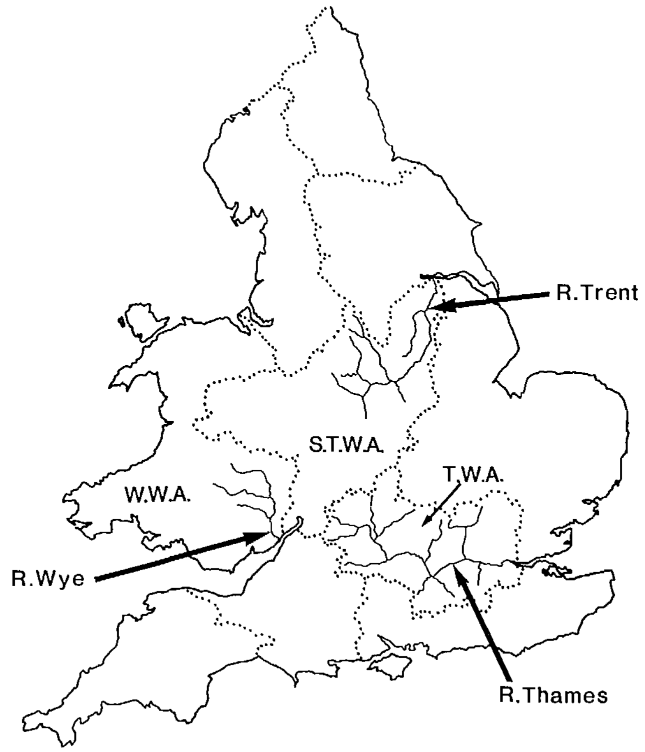

FIG 1. The location of the Rivers Thames, Trent and Wye in England and Wales; dotted lines indicate the ten Regional Water Authorities: TWA = Thames Water Authority, STWA = Severn-Trent Water Authority, WWA = Welsh Water Authority.

TABLE 1. Physical, chemical and demographic characteristics of the Thames, Trent and Wye catchments; chemical data are for sites at Teddington (Thames), Yoxall (Trent) and Sollar's Bridge, Hereford (Wye), discharge data are for sites near the tidal limits.

	Thames	Trent	Wye
Physical			
Length km	324	270	238
Catchment area ha × 10^5	13.4	9.2	4.3
Number of tributaries	15	10	9
Mean gradient ‰	0.47	0.73	1.40
Mean rainfall mm•yr^{-1} Upper	739	1100	2326
Lower	717	772	1011
Mean discharge m^3•d^{-1} × 10^6	5.6	6.9	6.0
Chemical			
pH	8.0	7.7	7.7
Conductivity μs•cm^{-1}	554	1039	156
B.O.D. mg•L^{-1}	2.9	4.0	1.78
Nitrate nitrogen mg•L^{-1}	7.97	9.28	0.96
Total alkalinity mg•L^{-1}CaCO$_3$	186.6	164.3	46.1
Demographic			
Population density No•ha^{-1}	9.0	6.0	0.47

the end of the last century, the River Wye salmon stocks had been severely reduced by overexploitation of adult and juvenile fish.

With the growth and spread of the human population, conflicts on river use became more intense. Fish weirs constructed, often in association with mills harnessing water power; these impeded navigation and were often blocked with rubbish. The Acts of 1662 and 1664 to make 'divers rivers navigable' improved matters only slightly, and already the Thames at London had severe pollution problems through the discharge of untreated sewage. Conditions in 1616 drew these words concerning Thames mud from the playwright Ben Johnson:

> 'Which, when their oares did once stirre,
> Belch'd forth an ayre, as hot as at the muster
> Of all your night-tubs, when the carts doe cluster,
> Who shall discharge first his merd-urinous load.'

The introduction of the water closet in the 18 century exacerbated the problems, particularly in the Thames and Trent, which were not tackled until after the London cholera epidemics of 1843 and 1848–49. By then no migratory fish could pass through the Thames at London, and the Trent salmon population was to disappear by the end of the century. The introduction of sewage treatment facilities improved matters temporarily, but were overtaken by the industrial expansion and further increases in human population. Increasing use of the Thames and Trent for commercial boats, domestic and industrial water supply and sewage disposal were often at the expense of fisheries. By the 1950's the tidal Thames was virtually devoid of fish and invertebrate life, as too was much of the upper Trent catchment where large industrial conurbations had developed. The Wye remained free from such extremes but, together with other rivers to the west of Britain, demands upon its water resources from industrial areas have continually increased.

The 18th and 19th centuries saw the development of an extensive inland waterway complex of canals and navigable rivers. River depths in the Thames and Trent were maintained by the removal of gravel beds, together with improved upkeep of weirs. The gradual replacement of flash locks with modern pound locks facilitated boat movement. These links between different river systems allowed ready interchange of fish species, and the slow-flowing canals were ideal habitats for the invasion of predominantly lowland river species, such as roach *Rutilus rutilus* (L.), bream *Abramis brama* (L.), and pike *Esox lucius* L. These canal populations, in turn, influenced the composition of river fish communities, particularly in the middle and lower reaches of the Trent.

Since 1974, the water industry of England and Wales has been managed by 10 Regional Water Authorities (Fig. 1), whose areas are based on major river basins. They have a statutory responsibility for water treatment and supply, sewage treatment and disposal, pollution control, flood alleviation plus recreation and amenities. These duties include an obligation to maintain and improve freshwater fisheries. In Britain, the latter comprise game fisheries (salmonid species), eel fisheries and coarse fisheries. The first two involve the retention of fish for food; most eels are caught commercially (nets, traps) whereas salmonids are caught by angling or by nets. In 1983, 22 % of the salmon and sea trout catches were by rods and 78 % by nets. In contrast, coarse fish are nearly all returned alive to the water after capture and are mostly of sport fishing interest. There is considerable resistance by most of the 1.75 million freshwater anglers in Britain to the commercial exploitation of coarse fish, though this is widespread on mainland Europe and was a common practice two centuries and more ago in Britain. Coarse fish anglers can be solitary, but many are involved in competitive angling, often for valuable prizes. Because they are generally static, many more of them can be accommodated per kilometre of river bank compared with the roving game fishermen. The coarse angling season, with minor local variations, extends from mid-June to mid-March, ostensibly to protect the spring spawning season, though some fish species spawn outside this period. Game fishing occurs from March to October (with the same avowed intention), also with regional variations.

River Thames

Morphometry, hydrology and major uses

The Thames (Fig. 2) rises from the Jurassic limestone and clays in the west of England, but much of its flow in the upper and middle reaches comes from the Cretaceous chalk aquifers. The river meanders eastwards, mostly through farmland, into the Tertiary sands and clays of the London Basin. Overall the gradient is low (0.47‰) compared with the Trent and the Wye (Table 1, Fig. 3). The low rainfall surplus over evapotranspiration losses results in very low stream powers. River velocities are further reduced by division of the river by locks and weirs into 44 sections above Teddington Weir (the tidal limit), each between 1 and 10 km long. All these phenomena, combined with the fine-grained but cohesive nature of river bank material, has produced a meandering river but one with very little channel migration. The division of the river into a series of slow-moving pools by weirs and locks is a marked contrast with the shallow, faster-flowing river of Roman times and earlier.

Although the water resources of the catchment are comparatively small, the Thames together with artesian supplies and the much smaller River Lee (Fig. 2) serves a population of 12 million people. This constitutes about one quarter of the population of England and Wales and includes the 7 million inhabitants of Greater London.

On average, 4.6 million $m^3 \cdot d^{-1}$ of river water is abstracted for domestic and industrial supply, and 4.3 million $m^3 \cdot d^{-1}$ treated effluent is returned; this compares with an average flow at Teddington Weir of 5.8 million $m^3 \cdot d^{-1}$. Variations in discharge are not great and, generally, maximum daily flows are no more than twice the annual mean daily flow, and minimum daily flows are little less than half. Existing storage reservoirs have a relatively small capacity and, in the drought year of 1976, water from the Mole and Hogsmill tributaries (not normally used for potable supplies) had to be pumped upstream over a weir to maintain water levels for abstraction. For a few weeks the Thames actually flowed upstream for a short distance!

Thus, water abstraction and sewage disposal are major stresses on the river environment. Nevertheless, the number of fish in the lower Thames has increased gradually since 1959 when only occasional eels were caught. In the 1970's the Beckton sewage works (c. 50 km downstream of Teddington Weir) were rebuilt and enlarged. Following the closure of several other smaller works, most of London's treated effluent now enters the Thames in its tidal waters. This, together with stringent by-laws controlling the discharge of pollutants into the river, is the principal reason for the amelioration. Anadromous fishes can now pass through the Thames at London to previously abandoned spawning grounds upstream, and the smelt *Osmerus eperlanus* L., once the object of a major local fishery, is reappearing in large numbers. Over 8000 were caught in the tidal

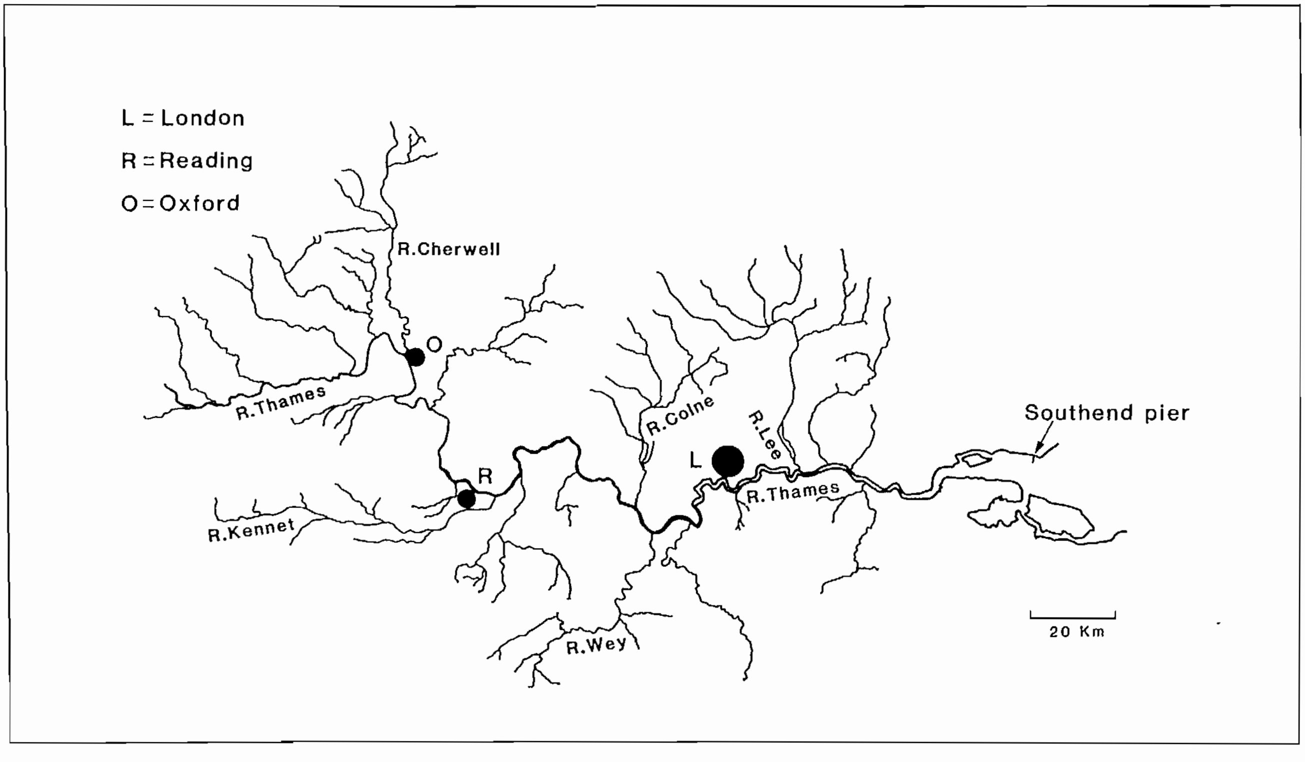

FIG. 2. The course of the River Thames showing the major towns and tributaries.

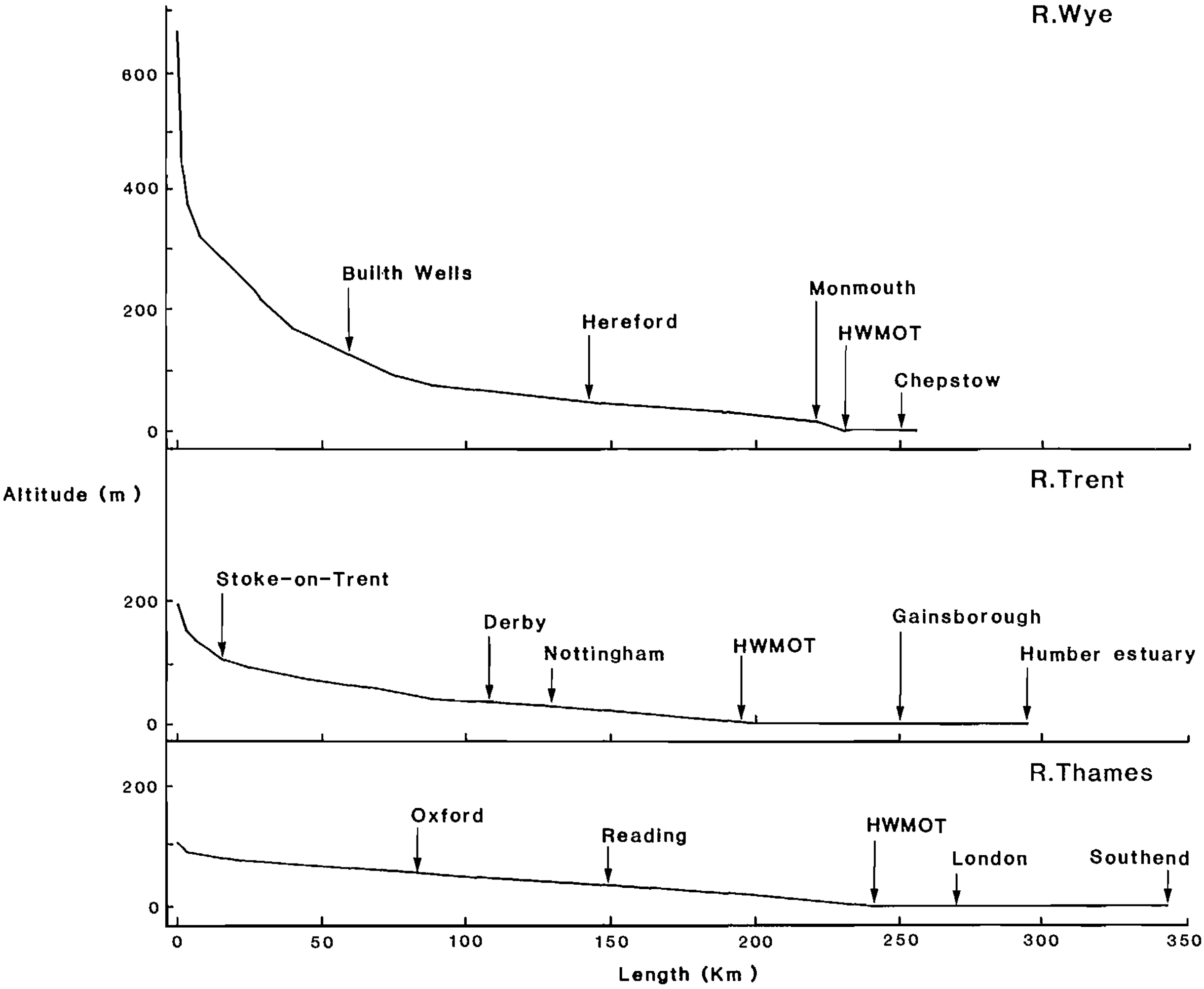

FIG. 3. Profiles of the Rivers Thames, Trent and Wye showing the upper tidal limit (HMWOT) and major towns.

reaches in 1983. Industrial development along the river now causes only minor problems, though continual surveillance of effluent quality at the many point sources has to be maintained.

Despite the political and public interest in the return of the Atlantic salmon, the middle and lower Thames is predominantly a coarse fishery, although the upper reaches and some tributaries are fished largely for non-migratory trout. In common with most of Britain, nearly all the fisheries are in private ownership, usually by angling clubs but occasionally by individuals or syndicates. They compete for recreational use of the river with the expanding pleasure boat industry. There is no legislative limit to the number of boats on the river and, in 1978, just under 30 000 craft were registered and about one million lock passages were recorded. Personal conflicts between anglers and boat-owners are relatively few, but bank erosion is a problem in some areas of the river. As a consequence, spawning and nursery areas for many species of fish are in backwaters, tributary streams or in the large weir pools. Bank protection, mostly wooden planking, is a feature of the Thames immediately upstream of Teddington Weir and nursery areas for 0 group fish are few in number.

Energy flow and fish production

Knowledge of the energy dynamics of the Thames biota centres around investigations made in the Thames at Reading during the 1960's and 1970's by Reading University. The results are summarized by Berrie (1972), Mann (1972) and Mann et al. (1972), and these publications form the basis of this summary.

The river profile in the area studied comprises a 50 m wide, 2–3 m deep, main channel with a clay substratum overlain with flints and chalk lumps. Shallow marginal areas, 10–15 m wide, support aquatic macrophytes, principally *Acorus calumus* (L.) and *Nuphar lutea* (L.) on the south bank, and *Salix* sp. trees on the north bank. The river is eutrophic, with an annual temperature range of 0–20°C.

The dominant primary producers are phytoplankton, followed by benthic algae and macrophytes. Allochthonous material, chiefly fallen leaves, is also an important source of organic material. Benthic invertebrates consist of filter feeders (Bivalvia, Porifera, Bryozoa), browsers and grazers (Gastropoda, larval Chironomidae) and predators (Hirudinea). The zooplankton community is small by comparison, but is a very important food source for 0 group fish. Terrestrial insects on the water surface, plus detritus and algae, are the major prey items for larger fish. Thus, in contrast to many rivers, most energy is derived from the water column and allochthonous sources, and comparatively little from the substratum. Production values for the various categories are given in Table 2.

Williams (1965, 1967) recorded 16 fish species from the Thames at Reading, dominated by the cyprinids, bleak *Alburnus alburnus* (L.) and roach. Together these formed 83 % of a seine net catch of over 11 000 fish. His production estimates, modified by more accurate data on fecundity and on population densities of 0 group fish (Mackay and Mann 1969; Mathews 1971), give a total of 198 k cal•m^{-2}•yr^{-1} (Table 2). About 70 % of this estimate is for 0 group fish, which rely chiefly on Rotifera, Cladocera and larval Chironomidae for food. Williams (1967) concluded that the very high population densities of bleak (2.5 fish•m^{-2}) and roach (1.0 m^{-2}) contributed to their low growth rates, largely because most food taken by fish was used in maintenance. He suggested that a reduction of fish stocks would result in enhanced growth rates, but no action was taken by angling clubs or the Water Authority to implement this recommendation.

The fish community at Reading is typical of the middle reaches of the Thames. Further downstream, below the tidal limit at Teddington but still in freshwater, the population is dominated numerically by the eel (50 %) followed by roach, perch *Perca fluviatilis* L. and dace *Leuciscus leuciscus* (L.) each 15 % and about 10 other species.

TABLE 2. Production at different trophic levels in the River Thames at Reading, based upon data given by Mann et al. (1972).

	k cal•m^{-2}•yr^{-1}	
Primary production		
Phytoplankton and seston	1907	
Periphyton and benthic detritus	462	Total = 2492
Aquatic macrophytes	44	
Allochthonous organic matter	79	
Secondary production		
Zooplankton	97	
Chironomidae	71	
Browsers and grazers	15	Total = 410
Filter feeders	11	
Predators	1	
Surface insects	215	
Fish production		
Bleak, *Alburnus alburnus*	105	
Roach, *Rutilus rutilus*	32	Total = 198
Other species	61	

Fisheries management

Although the upgrading of water quality in the lower Thames led to a resurgence of fish populations, the cleaning-up of the river was not aimed principally at improving fisheries. Restoration of fish populations resulted from natural immigration from relatively unpolluted reaches upstream or from some of the tributaries entering the tidal reaches. Even though the majority of the 450 000 anglers in the Thames area (Parton 1978) are coarse fish anglers, virtually no management of these fishes in the main river is attempted by Thames Water or local riparian owners. Some incidental protection of marginal habitats occurs through the concern over bank erosion by boat wash. However, the interest of Thames Water in this environmental damage is principally for flood protection and amenity aspects. Dredging of the main channel to facilitate navigation and land drainage is a continuous operation, and its effect on fish populations has been investigated on a small scale in some tributaries (Armstrong 1983; Spillet et al. 1985). Removal of in-stream and bank cover caused a substantial reduction (31–64 %) in densities of cyprinids, and removal of bottom clay material caused a diminution in food supply and spawning areas for some species. Rehabilitation of clay substrata is a lengthy process and the construction of gabions (underwater shelters) for fish and the introduction of crushed limestone and flints to encourage the development of invertebrate and macrophyte communities have had promising results. However, it is doubtful if such remedial measures will be practicable in the main river channel.

In the trout waters in the upper reaches of the Thames, and in some tributaries, removal of unwanted fish species by electric fishing is a common practice. Pike are removed to reduce predation, whereas dace and grayling *Thymallus thymallus* (L.) are culled to reduce their supposed competition with trout for food and space. However, evidence is increasing that some management practices are, at best, a waste of effort. For example, pike populations show homeostatic regulation and increased fishing mortality may be balanced by decreased natural mortality (Mann 1982, 1985).

Since 1979, Thames Water have concentrated much of their fisheries management resources on the rehabilitation of Atlantic salmon. This £65 thousand•yr^{-1} programme involves the annual stocking of, on average, 56 000 0-group salmon parr and 9 500 1-yr-old smolts into relevant parts of the Thames catchment. Initially, parr were obtained from hatcheries elsewhere in Britain, but current emphasis is on rearing eggs from returning adults in order to enhance the genetic integrity of the stock. The present annual run of adult fish is between 200 and 400, and some natural spawning has occurred. A few adults have even successfully negotiated weirs that previously were thought to be impassable. However, all adults examined are thought to have originated from stocked juveniles, with return rates being 0.68–0.84 % from those stocked as 0-group parr and 1.07–1.58 % from smolts.

Future work, aimed at establishing an annual run of 1 000 adults, will include the use of telemetry to assess upstream migration. Automatic recording of upstream migration by adult salmon, using resistivity counters is increasing in Britain (Hellawell 1973; Mann et al. 1983). Although salmon runs in the Thames will not reach pre-18th century levels in the near future, a potential management problem will be the conflicting interests of game (salmonid) and coarse fish anglers. Some anglers indulge in both sports, but most are distinct, with game fishermen generally belonging to the higher income brackets. Some coarse fish anglers have expressed fears that a full rehabilitation of salmon stocks will be to the detriment of coarse fishing, both biologically (interspecific interactions) and financially (coarse fish waters becoming too expensive to rent). Although salmon stocks in the Thames were once high, Wheeler (1979) suggests that the lowland nature of the river means that it would not have supported the very high numbers attributed to the river by some authors. Credence to this view is lent by records of salmon imports to London from northern England in the seventeenth and eighteenth centuries. Nevertheless, the return of salmon to the Thames is to be welcomed, both in its own right and as a symbol of the improved river environment.

River Trent

Morphometry, hydrology and major uses

The Trent (Fig. 4) has its source in the coal measures of the west Midlands, but most of its valley consists of Triassic Keuper marl. Two large southern tributaries, the Tame and Soar, flow through similar geological regions, whereas the Derwent and Dove to the north drain chiefly Carboniferous limestone. Unlike most British rivers, the catchment carries most of its 5.85 million population, with associated urban and industrial developments, around the upper reaches of the main river and tributaries. Up to the 1970's, the input of industrial and sewage effluent rendered parts of the Trent catchment devoid of fish life, especially the Tame tributary flowing from Birmingham. Industrial pollutants included clay suspension from potteries, organic effluent from breweries and a range of chemicals, including dissolved heavy metals such as copper, zinc, chromium, nickel and cadmium, from chemical and dye works. However, in recent years many factories have closed because of economic recession. This, in addition to increased investment in effluent treatment and the enforcement of pollution control legislation, has resulted in considerable improvements in water quality. Even so, the Trent shows a downstream improvement in conditions, largely through the dilution effects of the relatively clean northern tributaries. Accidental pollution and storm water overflows from urban areas can still cause occasional problems, and fish populations in the middle and upper reaches are still at risk. However, though some tributaries are affected, fish kills in the main river are now rare.

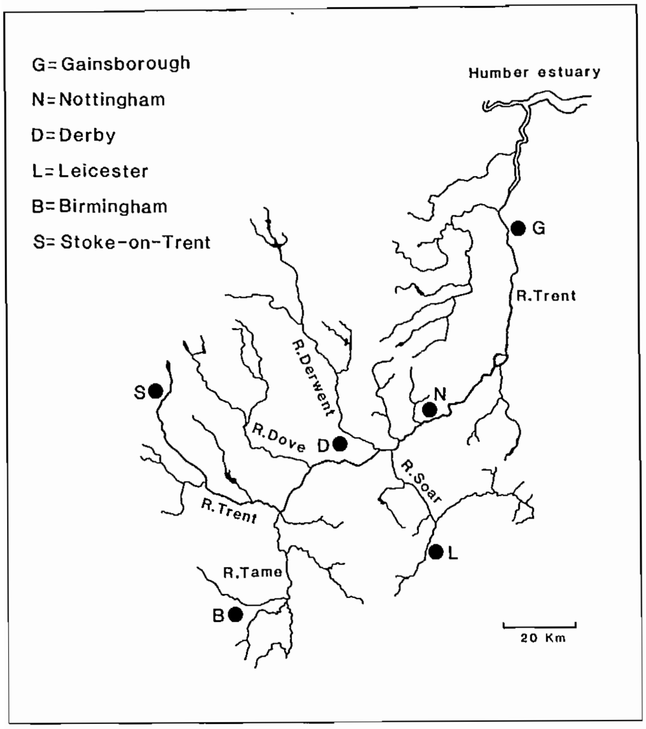

FIG. 4. The course of the River Trent showing the major towns and tributaries.

About one-third of Britain's electrical generation capacity (15 000 MW) is situated on the Trent, largely because of the proximity of coal deposits. The earlier power stations were cooled by once-through water circulation, which had the net effect of raising mean water temperatures in the middle Trent by 5°C. Natural river temperatures in Britain rarely exceed 24°C and the upper limit is normally in the 16–22°C range. But, below some power stations, water temperatures could reach 30°C, and Alabaster (1969) noted that some elevated temperatures in November exceeded normal summer temperatures. Today, many of these older stations are closed and the more recent ones are cooled by heat dissipation. Cumulatively they can reduce flows by up to 0.4 million $m^3 \cdot d^{-1}$, which is about 5 % of the mean flow near Gainsborough (Fig. 4).

Nearly all the potable supply is from reservoirs on the tributaries, especially those in the limestone areas, and virtually none is abstracted directly from the Trent. These supplies are insufficient to meet the demands of the region and water has to be imported from wetter areas to the west. Birmingham (population: 1 million) obtains most of its supply from the upper Wye via a 90 km long pipeline and the effluent goes into the R. Tame. This can have a marked effect on river flows, especially in dry weather conditions, and Tame flows can exceed those of the main river.

Commercial boat traffic (barges) is still prominent in the 130 km section from Nottingham to the Humber estuary. However, the adjoining canals are now the province of anglers and pleasure boats and are rarely used for carrying freight. In 1979, over 90 000 rod licences were sold in the Trent area, 90 % of them for coarse angling. Present day numbers are likely to be similar although, since 1979, separate records have not been kept for the different regions managed by the Severn–Trent Water Authority. In 1983, overall expenditure on fisheries by the Severn–Trent W.A. was about 0.5 % of the total annual expenditure of £231 million.

Fisheries management

There has been no study of the Trent (or any other large British river) that is comparable to study of the Thames at Reading. Restoration of water quality has been taken as the necessary prerequisite to detailed biological investigations, and the Trent Biotic Index (Woodiwiss 1964) was developed to monitor pollution levels using the diversity of macroinvertebrate communities. But most research on fish populations and other trophic levels has been confined to the tributary rivers. Main river studies have encountered sampling difficulties, especially where flows have been augmented, and angler catches have formed the basis of fish stock assessments. Between 1975 and 1981 the fish populations of the Trent catchment were surveyed (Severn–Trent Water Authority 1983) but electrofishing operations were confined to waters less than 20 m wide and 2 m deep. Here the standing crops, which were dominated by cyprinid species, ranged from 13 to 898 kg•ha^{-1}. The most important species were chub *Leuciscus cephalus* (L.), gudgeon *Gobio gobio* (L.), roach and dace. In adjoining canals, where roach dominated, the maximum standing crop recorded was 266 kg•ha^{-1}. In larger waters, including the main river, the survey relied on information from questionnaires sent to anglers. These provided data on changes in relative abundance, and showed an increase in the numbers of some species, notably carp *Cyprinus carpio* (L.), barbel *Barbus barbus* (L.), bream and perch. However, some decline in the populations of roach and dace was also observed. There was a range of growth rates for most species, which reflected the wide variety of habitats throughout the catchment. However, the food-limited growth observed in the Thames (Williams 1965, 1967) did not occur, and Cooper and Wheatley (1981) recorded roach growth rates higher than in most other U.K. waters. They also used mark–recapture estimates, based on catches by match anglers, to assess coarse fish densities and species composition in a 1 km section downstream of Nottingham. Roach, dace, bleak, gudgeon and chub over 100 mm in length had a combined density of 22 500 fish•ha^{-1} (447 kg•ha^{-1}), compared with 37 000 fish•ha^{-1} (476 kg•ha^{-1}) for roach, dace, bleak, perch in the Thames (Williams 1965, 1967). However, no data were obtained for young fish and these could make a considerable contribution to population density and production.

The results of the fishery investigations in tributaries have some relevance to the main river. Fisher and Broughton (1984) assessed the improvements to angler catches following the enhancement of cyprinid populations in the Derwent by stocking. Swales (1982) examined the degradation of a coarse fishery through land drainage operations, and obtained results similar to those reported by Armstrong (1983) and Spillett et al. (1985) for Thames tributaries. Preliminary studies of coarse fish movement, using ultrasonic tagging, in the Trent, Thames and other rivers suggest this to be a potentially rewarding line of research, especially if used in conjunction with the determination of fish stocking policies (Langford 1979).

The greatly improved status of the Trent, as exemplified by the substantial reduction in B.O.D. levels over much of the catchment, from c. 13 mg•L^{-1} O_2 in 1950 to less than 5.0 mg•L^{-1} by 1980, has been followed by many fish species extending their range. The spasmodic appearance of Atlantic salmon occasioned a feasibility study for its rehabilitation, and some fish passes on weirs have been constructed. Suitable spawning and nursery areas certainly exist in the Trent, but further progress will depend upon the level of financial investment by the Water Authority. Currently this programme is rated as lower priority than the maintenance and improvement of current coarse fisheries, and the development of commercial eel fisheries in the lower reaches of the river.

River Wye

Morphometry, hydrology and major uses

The Wye (Fig. 5) is currently the most important salmon river in England and Wales, with an average annual catch of about 5 000 fish. The fishery is very old, and basket weirs were in existence as early as the eighth century.

Many details concerning the river and its surrounds are given by Edwards and Brooker (1982, 1984). Its source is at an altitude of 677 m near Plynlimon, in an upper catchment area of impermeable Silurian and Ordivician rocks, principally shales and mudstones, but the lower catchment is mostly Old Red Sandstone. Unlike the Thames and Trent, the Wye catchment is sparsely populated; no towns exceed a population of 10 000 except Hereford which reaches almost 50 000. Most of the drainage area is agricultural land, with the uplands used largely for rough grazing and the richer soils of the lower valley devoted principally to mixed and dairy farming.

River flows are high and variable in the upper reaches as a consequence of the high rainfall (2500 mm•yr^{-1} at Plynlimon) and the impermeable rocks. A more stable flow regime is apparent further downstream where the rainfall is lower and less variable (660 mm•yr^{-1} at Hereford). Water for irrigation and potable supply is taken for regional use, and the former can affect dry weather flows. However, much of the precipitation in the upper catchment enters storage reservoirs and is piped to the industrial Midlands of England. Birmingham, in the Trent catchment, receives about 0.3 million m^{3}•d^{-1}, which represents 5% of the mean river flow at Monmouth (Edwards and Brooker 1982). Scope for further exploitation of the water resources clearly exists, but afforestation of the upper catchment has been suggested. The latter could more than double water losses through evapotranspiration and thus could affect river flows and water chemistry (Newson 1979; Egglishaw 1985). Thus, care is required to guard against impairment of the river environment through future developments. In fact, a

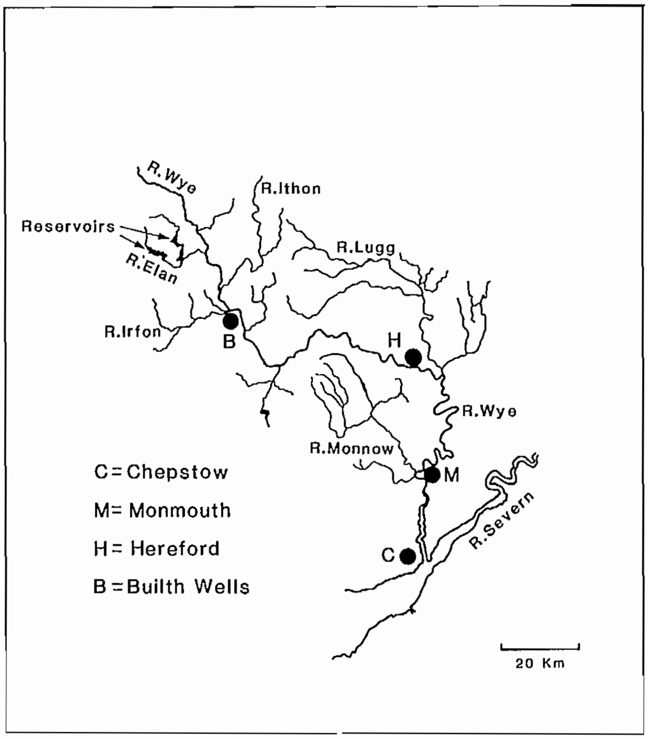

FIG. 5. The course of the River Wye showing the major towns and tributaries.

measure of protection already exists in that the whole Wye valley has been designated as a Site of Special Scientific Interest (SSSI) by the Nature Conservancy Council. Through the statutes of the Wildlife and Countryside Act this ensures that fishery and other conservation interests are kept informed of future plans for development, and are provided with limited legal protection against derogation of the river environment.

The lower Wye provides opportunities for angling and boating. In a survey of this and other rivers, O'Riordan (1978) found that roughly one-third of anglers had had one or more conflicts with boat owners. About one half of the boatmen interviewed recorded grievances with anglers. Increases in leisure time in the future may result in more frequent conflicts.

The Wye biota

The Wye catchment contains a range of habitats, which reflect the local geology and stream morphometry. The river becomes progressively rich in chemical nutrients as it passes from the impermeable strata to the softer sandstone rocks. This enrichment is enhanced by the input of sewage and the run-off from arable land, particularly with respect to phosphate and nitrate. Allied to the more stable flow regime, the eutrophication of the river is reflected by the high levels of primary production, chiefly macrophytes (e.g. *Ranunculus* spp., *Potamogeton* spp.) and benthic algae. In 1976, decomposition of large stands of macrophytes and the occurrence of high summer temperatures resulted in mass mortalities of adult salmon (Brooker et al. 1977).

Surveys of the invertebrate fauna have identified 227 different taxa, of which 44 per cent are Diptera (chiefly Chironomidae). Full details of these are given by Edwards and Brooker (1982) but, in general, the upper reaches are dominated by Plecoptera with Ephemeroptera, Trichoptera, Coleoptera and Diptera whereas Oligochaeta, Ephemeroptera, Trichoptera, Coleoptera and Diptera are the more important taxa downstream. Within these broad categories, a complex stratification of individual species occurs along the length of the river. Invertebrate densities range from 500 to 22 000 individuals$\cdot$m^{-2}.

Trout and salmon occur along most of the river, but the principal spawning areas are upstream of Builth Wells (Fig. 5). Studies by Gee et al. (1978a, b) found that production values ranged from 2.9 to 19.7 g$\cdot$m$^{-2}\cdot$yr^{-1} for trout and from 7.7 to 26.8 g$\cdot$m$^{-2}\cdot$yr^{-1} for salmon. They demonstrated a linear relationship between trout production and the general level of productivity, as indicated by the calcium concentration. This relationship explained about 72 % of the observed variation in trout production. Unlike the cyprinid studies in the Thames, production by 0 group fish accounted for less than 10 % of the production estimates (Milner et al. 1978a, b). No dietary studies on salmonid fish in the Wye have been published, but it is likely that the chief prey items are aquatic invertebrates supplemented by surface water insects. No production estimates are available for the non-salmonid species in the lower catchment, of which the dace, roach, chub, pike and grayling are the most important. Studies by Hellawell (1971a, d, 1972, 1974) showed the importance of macroinvertebrates, especially Chironomidae and *Simulium* larvae, in the diet of these fish species, supplemented by the moss *Fontinalis* and filamentous algae in chub and large roach.

The twaite shad *Alosa fallax* (Lacépède) and the larger allis shad *Alosa alosa* (L.) both spawn in the Wye, in May or June, as far upstream as Builth Wells. Most adults die after spawning and the young fish migrate downstream to the Severn estuary soon after hatching, though some may remain in the river until the following season (Claridge and Gardner 1978). The numbers of both species have declined greatly since the seventeenth and eighteenth centuries, when they were valued as much as salmon, and the allis shad is now rare. Navigation weirs may hinder spawning migration, and water abstraction for irrigation during dry weather can restrict spawning activity to the lower reaches of the river.

Fisheries management

Data concerning Wye fish come from the salmon catch records kept by J.A. Hutton from 1908 to 1939, which are among those analysed by Gee and Milner (1980). These latter authors were also involved in more recent studies of juvenile salmon in the Wye (Gee et al. 1978a, b). In addition Hellawell (1969, 1971a, b, c, d, 1972, 1974) described the biology of several coarse fish species in two Wye tributaries, the Afon Llynfi and River Lugg. In 1982, salmon licences for the Wye numbered 2214, compared with 5692 for non-migratory trout and 9467 for coarse fish and eels. However, the chief fishery interest by the Welsh Water Authority, which has the Wye under its jurisdiction, is in salmon. In 1982 the Authority spent about £1.28 million for fisheries maintenance and improvement in the whole of its area. Anti-poaching activities (20 %), habitat protection (28 %) and maintenance (26 %) accounted for most of this expenditure.

The overexploitation of salmon in the Wye only ceased at the end of the 19th century when net catches declined to such an extent that netting rights could be bought cheaply by the Wye River Authority. Recovery of stocks was rapid and catches have been continuously monitored since 1905. Analyses of 70 years catch data and age-composition statistics (Gee and Milner 1980) have shown that a decrease in net catches has been balanced by a seven-fold increase in rod catches. Age-composition changes since 1930 are reflected in a decrease in the mean weight of salmon caught. Prior to 1945, large three sea winter (3 SW) fish dominated the catches but now 1 SW (20 %) and 2 SW (60 %) salmon make up the bulk of the rod catch (Fig. 6). Gee and Milner (1980) suggested that overfishing of the run of large 3 SW fish early in the season was the probable cause of this change in age-structure. Subsequently, computer simulations were made of changes in the numbers of adult salmon, based on the assumption that sea-life duration is an inherited trait and adult mortality (marine and freshwater) is highest in older fish (Gee and Radforth 1982). The results paralleled the changes observed in the Wye and, since these changes preceded the expansion of the Greenland fishery, there is support for the idea that the river phase has been overexploited. However, recent evidence for some Scottish rivers has indicated a correlation between the relative proportion of 1 SW and older salmon with Arctic sea temperatures (Martin and Mitchell 1985). It is suggested that the recent colder periods have restricted the northern migration of

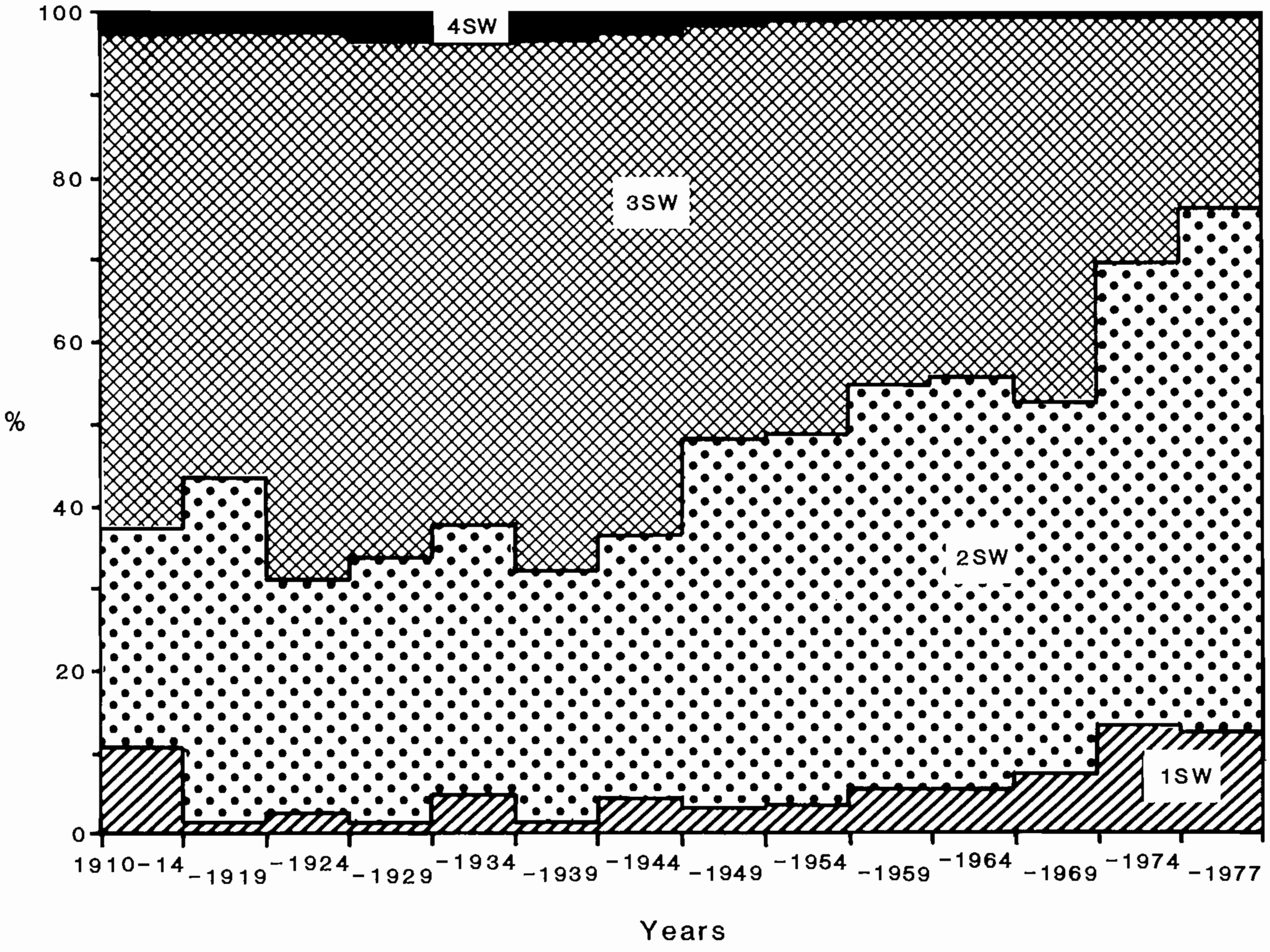

FIG. 6. The percentage numbers of 1-, 2-, 3- and 4-sea winter Atlantic salmon (*Salmo salar*) caught by anglers in the River Wye from 1910 to 1977 (reproduced from data given by Gee and Milner 1980, by permission of J. Appl. Ecol.).

salmon and caused them to remain in warmer seas. Hence growth rates have been more rapid and relatively larger numbers of fish have returned to the rivers as 1 SW fish.

Discussion

Together, the Thames, Trent and Wye epitomise most of the major management problems and practices encountered in British large rivers. The constraints of a small rainfall surplus in areas of high urban and industrial development caused, until very recent times, a massive deterioration in water quality in parts of the Thames and Trent catchments. Hence, the Regional Water Authorities have concentrated on upgrading the river environment, through vigorous pollution control and improved sewage treatment facilities. This amelioration has led, slowly, to the return of fish and other aquatic biota to areas previously devoid of such life. The prime example is the recovery of the Thames at London over the past 30 years.

Both the R.W.A.'s and fishing associations have adopted a passive policy regarding the management of coarse fish stocks in the main river channels, though some habitat modification and stocking is carried out in the tributaries. Some of these areas in the Thames and Trent catchments may be important as spawning and rearing zones for main river fishes. The work by Williams (1965, 1967) in the Thames at Reading was supported financially by a large angling association worried about the lack of large fish in the river, but the recommendation to cull stocks in order to increase the growth rates of perch and other species was never implemented. The role of environmental factors, which act through the early stages of the life-cycle, has been examined for several fish species in a number of rivers (Mills and Mann 1985). The results emphasised the need for more detailed knowledge of spawning and the habitat requirements of newly hatched fish. However, financial constraints have limited the amount of research on coarse fish populations, in contrast to that on salmonids, which have a high political profile and an influential lobby. Unlike the situation in many other European countries, there is little financial support by coarse fish angling interests for research on non-salmonid species.

More effort has been made in regard to the populations of Atlantic salmon. Thames Water Authority are committed to a long-term programme to restore salmon to the river, although such a restoration may conflict with coarse fishing interests. The Wye salmon stocks have maintained themselves since overfishing ceased at the turn of the century, and currently there is no enhancement of stocks from hatchery progeny. Such propagation is a feature of many other rivers in England and Wales, and in 1983 and 1984 about 1.5 million eggs, fry, parr and smolts were introduced each year into a variety of large and small rivers. Wye catch statistics are based on rod and net-caught fish and the evidence, accumulated since 1905, has revealed some marked alterations in age-composition. Whether these changes can be related to fishing effort (Gee and Milner 1980) or to changes in Arctic sea temperatures (Martin and Mitchell 1985), or both, is open to debate. Although the Wye becomes enriched in the downstream reaches, water quality is not a serious problem as regards the maintenance of the salmon fishery. A more acute problem is the degree of water abstraction, both for export to other regions and for local use. Land irrigation during dry weather can have a marked effect on river discharge, and fish mortalities under extreme conditions do occur (Brooker et al. 1977). Further demands on the water resources of the Wye catchment could increase the problem further, though the Wye's status as an S.S.S.I. may help prevent major changes. However, the example of the Thames shows the possibility of combining a high exploitation of water resources with the maintenance and improvement of fisheries.

Acknowledgments

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References

ALABASTER, J. S. 1969. Effects of heated discharges on freshwater fishes in Britain, p. 354–381. *In* P.A. Krenkel and F.L. Parker [ed.] Biological aspects of thermal pollution. Vanderbilt Univ. Press, Vanderbilt.

ARMSTRONG, G. S. 1983. Some effects of maintenance dredging on fish populations in a lowland river. Proc. 3rd Br. Freshw. Fish. Conf., Liverpool: 203–215.

BERRIE, A. D. 1972. Productivity of the River Thames at Reading, p. 69–86. *In* R.W. Edwards and D.J. Garrod [ed.] Conservation and productivity of natural waters. Symp. Zool. Soc. Lond., No. 29.

BROOKER, M. P., D. L. MORRIS, AND R.J. HEMSWORTH. 1977. Mass mortalities of adult salmon, *Salmo salar*, in the R. Wye, 1976, J. Appl. Ecol. 14: 409–417.

CLARIDGE, P. N., AND D.C. GARDNER, 1978. Growth and movements of the twaite shad *Alosa fallax* (Lacépède) in the Severn Estuary. J. Fish Biol. 12: 203–211.

COOPER, M. J., AND G. A. WHEATLEY. 1981. An examination of the fish population in the River Trent, Nottinghamshire using angler catches. J. Fish Biol. 19: 539–556.

EDWARDS, R. W., AND M. P. BROOKER. 1982. The ecology of the Wye. Dr W. Junk Publishers, The Hague, 164 p.

1984. Wye, p. 52–82. *In* B.A. Whitton [ed.] Ecology of European rivers. Blackwell Scientific Publications, Oxford.

EGGLISHAW. H. J. 1985. Afforestation and fisheries, p. 236–244. *In* J.S. Alabaster [ed.] Habitat modification and freshwater fisheries. Butterworths, London.

FISHER, K. A. M., AND N.B. BROUGHTON. 1984. The effect of cyprinid introductions on angler success in the River Derwent, Derbyshire. Fish. Manage. 15: 35–40.

GEE, A. S., AND N. J. MILNER. 1980. Analysis of 70-year catch statistics for Atlantic salmon (*Salmo salar*) in the River Wye and implications for management of stock. J. Appl. Ecol. 17: 31–57.

GEE, A. S., N. J. MILNER, AND R.J. HEMSWORTH. 1978a. The production of juvenile Atlantic salmon, *Salmo salar*, in the upper Wye, Wales. J. Fish Biol. 13: 439–451.

1978b. The effect of density on mortality in juvenile Atlantic salmon (*Salmo salar*). J. Anim. Ecol. 47: 497–505.

GEE, A. S., AND P. J. RADFORTH. 1982. The regulation of stock characteristics in a simulated Atlantic salmon population. Fish. Res. 1: 105–116.

HELLAWELL, J. M. 1969. Age determination and growth of the grayling *Thymallus thymallus* (L.) in the River Lugg, Herefordshire. J. Fish Biol. 1: 373–382.

1971a. The food of the grayling *Thymallus thymallus* (L.) in the River Lugg, Herefordshire. J. Fish Biol. 3: 187–197.

1971b. The autecology of the chub, *Squalius cephalus* (L.), of the River Lugg and Afon Llynfi. I. Age determination, population structure and growth. Freshw. Biol. 1: 29–60.

1971c. The autecology of the chub, *Squalius cephalus* (L.), of the River Lugg and Afon Llynfi. II. Reproduction. Freshw. Biol. 1: 135–148.

1971d. The autecology of the chub, *Squalius cephalus* (L.), of the River Lugg and Afon Llynfi. III. Diet and feeding habits. Freshw. Biol. 1: 369–387.

1972. The growth reproduction and food of the roach *Rutilus rutilus* (L.) of the River Lugg, Herefordshire. J. Fish Biol. 4: 469–486.

1973. Automatic methods of monitoring salmon populations (Int. Atlantic Salmon Symp., St. Andrews, Canada 1972). Spec. Publ. Atl. Salmon Fdn. 4: 317–337.

1974. The ecology of populations of dace, *Leuciscus leuciscus* (L.), from two tributaries of the River Wye, Herefordshire, England. Freshw. Biol. 4: 577–604.

LANGFORD, T. E. 1979. Observations on sonic tagged coarse fish in rivers. Proc. 1st Br. Freshw. Fish. Conf., Liverpool: 106–114.

MACKAY, I., AND K. H. MANN. Fecundity of two cyprinid fishes in the River Thames, Reading, England. J. Fish. Res. Board Can. 26: 2795–2805.

MANN, K. H. 1972. Case history: the River Thames, p. 215–232. *In* R. T. Oglesby, C. A. Carlson, and J. A. McCann [ed] River ecology and man. Academic Press, New York and London.

MANN, K. H., R. H. BRITTON, A. KOWALCZEWSKI, T.J. LACK, C.P. MATHEWS, AND I. MCDDONALD. 1972. Productivity and energy flow at all trophic levels in the River Thames, England, p. 579–596. *In* Z. Kajak and A. Hillbricht-Ilkowska [ed.] Productivity problems in freshwaters. Proc. IBP/UNESCO Symp., Kazimierz Dolny, Poland, 1970.

MANN, R.H.K. 1982. The annual food consumption and prey preferences of pike (*Esox lucius*) in the River Frome, Dorset. J. Anim. Ecol. 51: 81–95.

1985. A pike management strategy for a trout fishery. J. Fish Biol. 27 (Suppl. A): 227–234.

MANN, R. H. K., J.M. HELLAWELL, W.R.C. BEAUMONT, AND G.I. WILLIAMS. 1983. Records from the automatic fish counter on the River Frome, Dorset 1970–1981. FBA Occ. Publ., 100 p.

MARTIN, J.H.A., AND K.A. MITCHELL. 1985. Influence of sea-temperature upon the numbers of grilse and multi-sea winter Atlantic salmon (*Salmo salar*) caught in the River Dee (Aberdeenshire). Can. J. Fish. Aquat. Sci. 42: 1513–1521.

MATHEWS, C. P. 1971. Contribution of young fish to total production of fish in the River Thames near Reading. J. Fish Biol. 3: 157–180.

MILLS, C. A., AND R.H.K. MANN. 1985. Environmentally-induced fluctuations in year-class strength and their implications for management. J. Fish Biol. 27 (Suppl. A): 209–226.

MILNER, N. J., A.S. GEE, AND R.J. HEMSWORTH.
1978a. The production of brown trout, *Salmo trutta*, in tributaries of the upper Wye, Wales. J. Fish Biol. 13: 599-612.

1978b. Recruitment and turnover of populations of brown trout, *Salmo trutta*, in the upper Wye, Wales. J. Fish Biol. 15: 211-222.

NEWSON, M. D. 1979. The results of ten years' experimental study on Plynlimon, Mid-Wales, and their importance for the water industry. J. Inst. Wat. Eng. Sci. 33: 321-333.

O'RIORDAN, T. 1978. Angling and boating, p. 117-134. *In* J. S. Alabaster [ed.] Recreational freshwater fisheries. Water Research Centre, Medmenham, England.

PARTON, D. 1978. Statutory control and planning in relation to water recreation and freshwater fisheries, p. 85-98. *In* J. S. Alabaster [ed.] Recreational freshwater fisheries. Water Research Centre, Medmenham, England.

SEVERN-TRENT WATER AUTHORITY. 1983. Review of fisheries survey undertaken in the Trent area of the Severn-Trent Water Authority during the period 1975-1981. Severn-Trent W.A., Directorate of Technical Services Fisheries Section, Nottingham, 122 p.

SPILLETT, P. B., G. S. ARMSTRONG, AND P. A. G. MAGRATH. 1985. Ameliorative methods to reinstate fisheries following land drainage operations, p. 124-130. *In* J.S. Alabaster [ed.] Habitat modification and freshwater fisheries. Butterworths, London.

SWALES, S. 1982. A 'before and after' study of the effects of land drainage works on fish stocks in the upper reaches of a lowland river. Fish. Manage. 13: 105-114.

WHEELER, A. 1979. The tidal Thames. Routledge & Kegan Paul, London. 228 p.

WILLIAMS, W. P. 1965. The population density of four species of freshwater fish, roach (*Rutilus rutilus* (L.)), bleak (*Alburnus alburnus* (L.)), dace (*Leuciscus leuciscus* (L.)) and perch (*Perca fluviatilis* L.) in the River Thames at Reading. J. Anim. Ecol. 34: 173-185.

1967. The growth and mortality of four species of fish in the River Thames at Reading. J. Anim. Ecol. 36: 695-720.

WOODIWISS, F. S. 1964. The biological system of stream classification used by the Trent River Board. Chem. Ind. (Lond.) 11: 443-447.

The Danube River and its Fisheries

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Abstract

BACALBAŞA-DOBROVICI, N. 1989. The Danube River and its fisheries, p. 455–468. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The Danube is the second largest river in Europe, with a catchment basin of 817 000 km^2, and an average annual discharge of 6 000m^3•s^{-1} (at Ceatalul Chiliei). The basin is industrialized and has a population of 70 million people. The river flows through eight countries, although the entire catchment basin lies within ten. Its fisheries have been known for more than 2 000 years. There are over 100 species of fish presently in the Danube, about 30 of which are commercially important. Roughly 30 000 t of fish are caught yearly by commercial and sport fishermen. Damming, construction of reservoirs, intense water pumping, sand and gravel extraction, navigation, and pollution by sewage and other contaminants, have created problems for the exploitation of the Danube fisheries. Loss in natural fish production has been partially compensated by legislation, management practices, aquaculture and international collaboration. Fisheries yields have generally been maintained and even enhanced in the lower Danube, mainly through aquaculture, and the introduction of exotic species.

Résumé

BACALBAŞA-DOBROVICI, N. 1989. The Danube River and its fisheries, p. 455–468. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Le Danube est le deuxième fleuve d'Europe; son bassin versant mesure 817 000 km^2 et il a un débit annuel moyen de 6 000 m^3•s^{-1} (à Ceatalul Chiliei). Le bassin versant est industrialisé; on y trouve 70 millions d'habitants. Le fleuve passe dans huit pays, mais le bassin versant s'étend dans dix pays. Ses richesses halieutiques sont connues depuis plus de 2 000 ans. Actuellement, on y trouve plus de 100 espèces de poissons, dont 30 environ sont importantes au point de vue commercial. Les captures annuelles de la pêche commerciale et de la pêche sportive représentent environ 30 000 tonnes de poissons. Les barrages, les lacs de retenues, le pompage d'importantes quantités d'eau, l'extraction de sable et de gravier, la navigation et enfin, la pollution par les eaux usées et d'autres contaminants, nuisent à l'exploitation des richesses halieutiques du fleuve. La législation, les modes de gestion, l'aquiculture et les plans de collaboration internationale ont compensé en partie la perte de production naturelle. En général, la productivité des pêches s'est maintenue et a même augmenté dans le cours inférieur du fleuve, essentiellement en raison de l'aquiculture et de l'introduction d'espèces exotiques.

Danube Fisheries

Location

The Danube River is situated in central and southeast Europe, in a catchment basin extending between 50° and 42°N. Its catchment basin of 817 000 km^2 is 1 630 km long from west to east, has a maximum breadth of about 600 km (Banu 1967), and is situated largely in natural forest zones except for the Panonian lowland and the Bǎragǎn east plains. Climatically, over two-thirds of the Danube catchment basin lies within the Cfb zone, one-fifth in the Dfb, and about one-twentieth in the Cfa. The remainder is characterized by high montane climate (Strahler 1969) (Fig. 1).

The Danube is the second longest river in Europe (2 857 km) and has a variable flow of between 1 650 to 17 750 m^3•s^{-1} at Ismail Ceatal (Mociornita 1958). Limnologically the Danube has been well-studied, being the subject of systematic international research by riparian countries.

Towards the end of the Nineteenth and the beginning of the Twentieth Centuries, the lower Danube fisheries were organized by ecological principles derived from studies by Grigore Antipa (1911, 1916, 1935). Hydrobiologist, zoologist, ichthyologist, economist, and prominent entrepreneur in other fields of activity, he proposed a theory for fishery productivity from floodplain rivers, and outlined agro-aquacultural management plans for large river floodplains on the basis of his Danube experience. In 1967 UNESCO (Bacescu 1967) celebrated the centenary of his birth.

History

Records of the Danube fisheries date back to 335 B.C. (Giurescu 1964), when the fish of the lower Danube were commercialized by the ancient Greeks. In the middle (Panonian) Danube basin, there were 4 000 fishermen on the Tisza River during the Twelfth Century, most from the town of Szeged. During the Middle Ages, complex legislation concerning fishing rights for the Danube floodplain lakes included provisions for their maintenance in good condition.

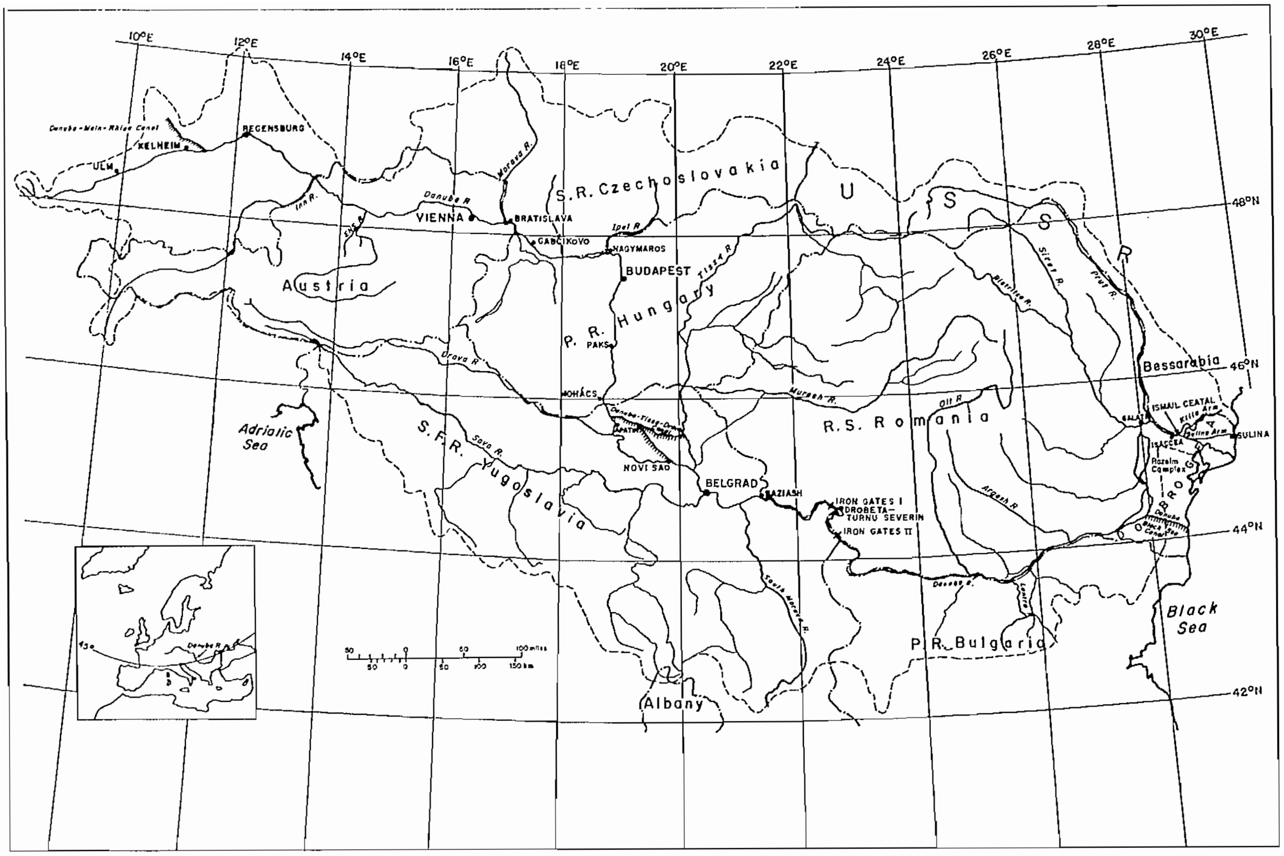

FIG. 1. Catchment basin of the Danube River.

Political instability in the region, due to opposing interests of three expansionist Empires (Ottoman, Russian, and Austrian) retarded economic development and its consequent ecological impacts. Deterioration of the environment, however, became significant only after the mid-Nineteenth century. Since 1850, damming and drainage of the middle catchment basin of the river affected nearly 4 million ha (Vidrascu 1921) and, by 1950, these works were extended to include more than 0.6 million hectares of the lower Danube.

The Danube originates in West Germany and flows through Austria, Czechoslovakia, Hungary, Yugoslavia, Romania, Bulgaria, and the USSR. One of the most important tributaries, the Inn originates in Switzerland. Small portions of the Danube catchment basin are also located in Poland and Albania. In Switzerland, West Germany, Austria, and in the last two decades, in Czechoslovakia, sport fishing and individual commercial fisheries are more prevalent than the state and cooperative fisheries dominant in other Danubian countries. The population in the catchment basin is now over 70 million.

At present, countries in the Danube basin permit fishery exploitation of the river according to national regulations but have regionally negotiated elements. Czechoslovakia, Hungary, Yugoslavia, Bulgaria, Romania and the USSR coordinate their Danube fishery policy through recommendations of the Joint Commission for the Application of the Fishery Convention in the Danube, signed in 1958 in Bucharest. The Joint Commission recommends minimum size limits, fishing seasons, the introduction of new fishing gear and methods. The application of the recommendations is subject to the authority of each country. On the whole, for a large international agency, with normal debates and temporary disagreements, its work is positive. Scientific investigations are carried out by both national institutions and the International Association of the Research of the Danube (affiliated with the International Association of Theoretical and Applied Limnology), to which all the riparian countries belong.

Major Stresses

Damming of the river has limited fish migration and altered habitat, creating conditions unfavourable to the dominant groups of phytophilous species. Pumping for irrigation and industry has extracted much biological material along with the water. The extraction of sand and gravel from the Danube channel has created zones with heavy turbidity. Sewage and other pollutants pose additional problems for the Danube fisheries.

Only slower flowing river-reaches freeze in some years, but during severe winters, when ice is thick and persistent, there are heavy losses of fish, not only in shallow waters of the floodplain, but also in many fish ponds constructed in the last decades on the dammed floodplain and delta.

Morphometry and General Description

The Danube is usually divided into three regions. The upper region from the source to Vienna (890 km) comprises

3 subdivisions; the headwaters, (Baden-Würtemberg reach), the Bavarian, and the Austrian subdivisions. The middle region from Vienna to the first Iron Gates barrage (993 km) has 3 subdivisions, from Vienna to Mohács, Mohács to Zemun and from Zemun to the Iron Gates I barrage. The lower portion from the Iron Gates I to the mouth (942 km) also has 3 subdivisions: the Iron Gates II reservoir, from its barrage to Galati, and then to the Black Sea.

Upper reaches of the river generally have the features of regulated streams (Herzig 1984). There are six dams between the source and Ulm and a further 17 dams between Ulm and Kelheim. At Ulm the mean annual flow is 48 $m^3 \bullet s^{-1}$ and sediment deposition is likely (Weber et al. 1974). The river is polluted between Kelheim and Regensburg, although water quality improves downstream. The river bottom, initially rocky, rapidly becomes covered with organic mud in the dammed reaches where the slope of the channel is very slight. In the Austrian reaches there are six dams (out of a proposed 13). Within the undammed zones the mobile, gravelly bottom produces low benthic populations, but the more stable reservoirs support a rich benthos.

Middle reaches of the river are flanked by two floodplains: Bratislava–Györ and Paks–Baziash. The former has a slope of 0.31 % with a highly variable flow regime. Here the river transports 630 000 m^3 of gravel and 7 million t of suspended matter annually and the bottom is unstable (Holcík et al. 1981). The floodplain has an area of 23 000 ha but will be dried by the lowering of the ground water. The Paks–Baziash floodplain receives the main tributaries of the Danube: Drava, Sava, and S. Morava from the south and Tisza from the north, all of which formerly had their own extensive floodplains. Approximately 4 million ha were impounded and drained in the Nineteenth Century, leaving only the Mohács-Apatin floodplain with a slope of 0.05 % and a total inundated area of 42 000 ha (Janković 1971). The Danube–Tisza–Danube canal has contributed to the isolation of the floodplain, cutting off several lakes with depths of up to 6 m. Oxbows of the middle Danube from Budapest to Baziash are in contact with the river from mean to high water only.

The reservoir formed by the Iron Gates I dam is 270 km long. The lower 50 km are lacustrine in character with depths of over 30 m and a low flow; upstream the character becomes increasingly riverine.

The Iron Gates II dam, in the lower reaches of the Danube is situated 80 km downstream of Iron Gates I. Between this dam and the delta, the river receives several tributaries including the Olt, Argesh, Siret, and Prut. All of these have storage reservoirs on them and as a result alluvial transport has decreased considerably in recent years (Miron 1983). The floodplain here previously exceeded 500 000 ha, but only 15 % of this area is still seasonally inundated. In particular, the islands of Borcea and Braila, which previously formed an internal delta of some 150 000 ha have been completely reclaimed.

The early state of the delta, when over 400 000 ha were flooded, was described by Mirica (1956), Leonte (1965) and the monograph of Banu (1967). Now the Danube delta (460 000 ha) has been completely transformed. Most western parts of the riverine-delta have been dammed or are about to be. The lakes of the northern delta and the Razelm complex to the south have controlled aquatic regimes. Tens of thousands of hectares of ponds have been built or are under construction in the central delta to compensate for the loss of fisheries from floodplain water bodies. Only the maritime delta has not been so heavily transformed; however, the canal transporting Danube water to Lake Sasik (20 000 ha) completely replaced the salt water of the lake by freshwater from the Danube (Mogiltshenko and Suchojwan 1985) thus extending the sea-riverine or maritime delta.

Chemistry

The Danube belongs to the hydro-carbonate series of rivers, but shows modifications along its length, consistent with changes in terrain from the moist headwater zone to the drier steppe downstream. In the main channel, at the Austro-Czechoslovak frontier, chlorides were 17 $mg \bullet L^{-1}$ and nitrates 3 $mg \bullet L^{-1}$ (Stanojević 1982). Near Russe (Rojhdestvensky 1968, 1979) NO_2 was recorded to be 1.0–18.0 $mg \bullet L^{-1}$, and total dissolved solids (TDS) ranged between 287 and 384 $mg \bullet L^{-1}$. All ions have maximal values during the autumn. In the delta TDS varies between 174 and 475 $mg \bullet L^{-1}$ (Romanenko et al. 1982). The Danube transports an average of 325 $g \bullet m^{-3}$ of suspended matter. The specific conductance of the upper middle Danube is variable for example:

Swiss Inn 131–232 μS,
Danube at Budapest 451 μs, and
Iron Gates Reservoir 323–383 μS.

There is evidence that a slow increase in dissolved salts is occurring from year to year (Ivanov 1982; Strainer et al. 1982). There is generally a large quantity of organic matter on the floodplains of the main channel and the delta. In delta lakes organic substances are stored in various forms; 3–8 % in floodable soil humus and 35–40 % in floating reed islands (Roman et al. 1982). pH varies between 7 and 8, with values as low as 6.5 during the ice cover. In the northern part of the delta, pH ranges between 7.7 and 9.7.

The waters of the Danube system are well oxygenated in the mountainous tributaries and high dissolved oxygen levels are maintained throughout the headwaters. However, many tributaries which are polluted have an O_2 deficit. For instance, the lower Sava has an average dissolved oxygen (DO_2) of 5.3 $mg \bullet L^{-1}$, only 44 % saturation (Matonickin et al. 1975). Delta lakes which connect with the main channel only at high water show a greatly reduced DO_2 tension at 3.2–3.5 $mg \bullet L^{-1}$ during their period of isolation. A severe shortage of DO_2 occurs in all stagnant waters under ice cover. Almost all of the Danube may be considered beta mesosaprobic (Marcoci and Cure 1981).

Primary Production

Bacterioplankton are most abundant during high water but a general trend of year-to-year increases in bacterial numbers has also been noted. Self-purification processes are active (Gawrischowa 1982), but proceed more slowly in stagnant areas (Nicolescu 1982).

Diatoms are the dominant elements in the phytoplankton of the upper Danube. In the lower Danube, peak abundance of phytoplankton occurs in autumn (Marcoci and Cure 1981). In floodplain lakes primary production by phytoplankton is highest in years of early and persistent flooding. Plankton production has increased throughout the Danube in recent years as the result of eutrophication.

In the middle and lower Danube, epiphytic algae occur in great numbers in lakes and reed beds, where they represent an important food source.

The main channels are devoid of vegetation because of rapid current, turbid water and frequent changes in water level. Vegetation type on the floodplain depends upon the height of the plain and the degree to which it is flooded. At the level of the Somova–Parkesh floodplain complex and downstream, floating reeds (''plaur'') are distributed throughout the delta. The most extensive and abundant aquatic vegetation is found on the delta where the extent of freshwater macrophytes is limited by the penetration of the saline tongue (Klokow 1982).

Riparian forests are usually discontinuous galleries of alder, oak and poplar in upstream and partially middle reaches, and of willow, poplar, and planted poplar downstream. Islets are either wooded or, as on the larger islands with interior lakes, covered with willows. Downstream, submerged roots of willow provide support for phytophilous fish eggs.

Secondary Production

Benthic fauna is generally well-developed on hard stable bottoms. Petran and Kothé (1975) showed that the density of animals on mobile substrates increased as water level and speed of current at the bottom were reduced. The composition of the benthic fauna has changed considerably following the closure of the Iron Gates I dam. Colonization by Caspian species in the Czechoslovakian and even Austrian and W. German parts of the river has increased. For instance *Hypania invalida* (Polychaeta), *Jaera sarsi* (Isopoda) and *Corophium curvispinum* (Amphipoda) were found even at Vilshofen, 2 250 km from the river mouth. In the reservoir itself, 40 % of the benthic fauna were new forms (Zinevici 1982) with a biomass of 21 g•m^{-2}. Between the Iron Gates reservoirs and the delta, the benthonic biocenoses are mainly sand and clay based. Russev (1981) recorded the average biomass from various types of bottoms for the Bulgarian stretch of the Danube that can be extrapolated for the right river of that subdivision as:

Bottom type	Biomass (g•m^{-2})
stones	72.5
mud	47.5
clay	26.4
sand	0.243

The various arms of the Danube delta have differing benthic biocenoses, thus the delta is uncommonly rich in benthic species.

The benthic fauna on the remnants of the lower Danube floodplain consist mostly of Chironomidae, Oligochaeta and Mollusca with biomass varying between 9 and 19 g•m^{-2}. The Danube delta has a large number of niches and a corresponding diversity of species. Faunal composition of the lake depends on salinity. In freshwater lakes, benthos is abundant but declines as salinity rises. For instance, benthos of the Razelm is much richer in recent years due to the decrease in salinity (28.6 g•m^{-2} in 1982 and 37.7 g•m^{-2} in 1983) and subsequent biomass increases especially through development of molluscs (Munteanu 1984). The marine fringe of the delta is rich in benthos and thus important for fish-fry. Zooplankton, important for juvenile fish, is more frequent in floodplain habitats and contributes to the river.

In addition to normal benthic fauna, the decapods, *Pontastacus cubanicus danubialis*, *P. leptodactylus salinus* and *P. eichwaldi danubialis*, which are not traditionally included in this category, are found particularly in lower reaches of the Danube (Brodskij 1982).

In the lower Danube and especially in its delta, two species of frogs, *Rana ridibunda* and *R. esculenta* are economically important (Bacalbasa 1966). As well, certain ichthyophageous birds, including pelicans (*Pelecanus onocrotalus* and *P. crispus*), the great cormorant (*Phalocrocorax carbo*), the Colymbiformes, the Ardeidae, and most Laridae are also important because of their predation on fish.

Hydrology, Hydraulics, and Effects on Fish Production

The hydrological regime of the Danube is complex. The upper Danube is heavily influenced by Alpine tributaries, particularly by snow melt which produces high water between May and July. Generally, the channel width is less than 250 m. Under mean-flow conditions, current velocity reaches 2.4–2.7 m•s^{-1}, but in impoundments it is slowed to as little as 0.3 m•s^{-1}. In the Austrian sector, oxygen levels are generally sufficient in reservoirs (Herzig 1984). Conditions are favourable for zooplankton in reservoirs of the upper Danube (Naidenov and Saiz 1975), where benthos is also enriched (Russev 1982). The complete isolation from the river of the now reduced floodplain and most oxbows, combined with decreased water temperatures in river channels, however, have reduced the number of fish species (Jungwirth 1984). Management for navigation has also been unfavourable for fish through usually more rapid flow and less diversified habitat. However, rubble-consolidated banks provide shelter for some fish species and a substrate for food organisms.

In the middle Danube the channel is between 200 and 300 m wide at its upper end. Discharge is highly variable with a mean of 2 000 m^{3}•s^{-1} and a mean velocity of 1.73 m•s^{-1}. Flows may increase to 8 000 m^{3}•s^{-1} with a velocity of 3.13 m•s^{-1} (Holčík et al. 1981). The turbidity of the water is very high and average maximum temperatures have increased to about 17.5°C. High water is in May–June in this reach and then the discharge decreases gradually for the remainder of the year. In the lower part of the middle Danube mean flows peak at 6 000 m^{3}•s^{-1}, the width of the channel is between 600–1 000 m and the water is clearer and warmer.

Fish yield from the isolated floodplain areas has declined (Djisalov and Tóth 1978–79). The Gabčikovo-Nagymaros River Barrage System currently under construction at the upper end of the middle Danube, will cause further losses in fish yield on the Czechoslovakian side; losses are estimated at 64–27 % of optimum; losses on the Hungarian side are expected to be even more severe (Tóth 1983). The Iron Gates I barrage was erected in 1969 at the lower limit of the middle Danube. In the first years following construction, the ichthyomass was less than in the non-dammed river. For example, mean catch per unit area in the Yugoslavian part of the reservoir from 1973 to 1978 was 63 % lower than catches in unregulated reaches (Holčík et al. 1981), and the same was true for the Romanian part of the reservoir. However, catches have since improved and from 1980 to

1985 total catch in this section was three times greater than that of the undammed Danube between 1959 and 1966 (Bacalbasa and Petcu 1969a).

Channel width in the lower Danube varies between 800 and 1 200 m. Depth ranges between 1.2 and 24 m, but a navigable channel 8 m deep is maintained downstream of Brăila. The mean discharge of the Danube increases slowly from 6 200 $m^3 \cdot s^{-1}$ in the upper reaches to 6 439 $m^3 \cdot s^{-1}$ at the mouth. Currently, velocity in the channel is about 0.76 $m \cdot s^{-1}$ at low flow, 1.16 $m \cdot s^{-1}$ at moderate flow and 1.59 $m \cdot s^{-1}$ at high flow. The Danube–Black Sea Canal has no influence on river flow; however, a change in water regime took place after the installation of the Iron Gates dams and floodplain longitudinal dikes. The high water level mark was increased by about 0.6 m and flow velocity was also increased.

In 1921, river length (km) to floodplain (ha) ratio was 1:612 between Drobeta–Turnu Severin and the delta, but by 1976 this was reduced to 1:118 (Bacalbaşa 1978). Fish living in the avandeltas and/or in the deltas, which migrate tens or hundreds of kilometres upriver to spawn in the Caspian and Black Sea region, are called semi-migratory. Fish of the Danube delta formerly spawned mostly in the floodplain between Galati and Călăraşi which is now dammed. Thus, no migrations occur and fish are reduced in number (Bacalbaşa 1980). Pumping stations are most numerous in this sector, with water pumped from near the river bank from May to July–August when fish have spawned and juveniles are present. Lakes supplied mostly with Danube water have a high percentage of typically Danube species (Bacalbaşa 1982) and fish transferred by pumping are also found in irrigation canals.

In the delta the longitudinal water supply was dominant, enhanced through specially constructed canals. Construction of short lateral canals, generally perpendicular to the first ones, has produced great siltation. Owing to deposition of dredge spoil near the new canal banks and to floating and submerged vegetation in the canals and channels of the river-delta, lateral water supply is now dominant. Through siltation, lakes have a reduced accessibility for fresh water and worsened ecological conditions (Breier 1979). Concomitantly, the erosion of the offshore bar to the south of the Sulina jetties, most marked in the zone of the Imputita canal (Spataru 1979), now allows penetration by sea water toward lakes Rosulet and Rosu during prevailing east winds, impoverishing the fauna of part of the marine delta. Furthermore, the USSR project to pump to 23.6 $km^3 \cdot yr^{-1}$ of fresh water from the Kilia arm (Romanenko et al. 1980) will also enhance seawater penetration.

Aquatic plants are dominant in the marshy delta, but of the 86 000 ha Razelm complex, 76 000 ha are open water. At present, the whole northern Razelm unit has been transformed into a freshwater basin to serve as a reservoir for irrigation of northeast Dobrogea. The same changes occurred for Sasik Lake, to the north of the delta, for the irrigation of the South Bessarabia.

Fish and Fisheries

Fish Species

With over 100 species the Danube is the richest river faunistically of the entire zoogeographical area (Banarescu 1964; Bacalbasa-Dobrovici et al. 1984). When marine species penetrate into the Danube discharge zone, the following families are represented: Petromyzontidae plus 23 fish families; 15 freshwater, 2 introduced, 3 migratory, and 4 brackishwater. The richest in species are Cyprinidae (39), Percidae (11), Gobiidae (11), Cobitidae (8), Salmonidae (7) and Acipenseridae (6) (Table 1). About one-third of the families have direct economical importance. *Anguilla anguilla*, the only catadromous species in the Danube, is maintained by stocking with elvers from Western Europe.

During the last century, some Danube fish species became more widely distributed naturally in the Danube system. For example, *Pelecus cultratus* reappeared and *Proterorhinus marmoratus* appeared in the upper Danube. In the first quarter of this century, *Carassius auratus* appeared in the river, and in the 1970's became one of the dominant forms. The majority of new fish species, however, were introduced by man: *Ictalurus nebulosus, Lepomis gibbosus, Salmo gairdneri, Salvelinus fontinalis, Coregonus lavaretus* and, in the last 25 years, the East Asian *Ctenopharyngodon idella, Hypophthalmichthys molitrix, Aristichthys nobilis* and the accidentally introduced *Pseudorasbora parva*. Many of these species have to be maintained by hatcheries, (e.g. *Salmo gairdneri, Coregonus peled, Micropterus dolomieui*, East Asian Cyprinids), for stocking into the river and/or oxbows.

Some indigenous Danubian migratory species, such as *Salmo trutta labrax* now have a reduced distribution, and others (*Acipenser sturio* and *A. nudiventris*) have disappeared.

Distribution

Upper Danube (890 km)

The Baden–Würtemberg reach (partially Swabia), is initially characterized by trout (*Salmo trutta fario*), which is succeeded by *Thymallus thymallus, Barbus barbus, Leuciscus cephalus,* and *Rutilus rutilus* (Torke 1985). In the Bavarian subdivision, *Barbus barbus* and *Chondrostoma nasus* are initially dominant but are replaced by *Leuciscus idus, Vimba vimba, Abramis sapa* and *A. brama*. The Austrian subdivision (down to Vienna, 265 km) is also dominated by *Chondrostoma nasus, Barbus barbus* and *Vimba vimba*, but *Stizostedion lucioperca* and *Acipenser ruthenus* also appear. Most of the larger Danube tributaries (Sava, Drava, Tisza, Morava, Olt, Siret, Prut) have similar zonations.

Middle Danube (993 km)

From Vienna to Mohács, the most frequently encountered species is *Barbus barbus* followed by the breams: *Abramis brama, A. sapa* and *A. ballerus; Stizostedion lucioperca* and *Perca fluviatilis* are also important. In the second subdivision (Mohács to Zemun), breams and *Cyprinus carpio* are dominant; *Barbus barbus, Stizostedion lucioperca,* and *Silurus glanis* are well represented and *Ctenopharyngodon idella* and *Hypophthalmichthys molitrix* are frequently encountered. The lower subdivision, from Zemun to the Iron Gates I barrage, is located in the Iron Gates I reservoir; here breams, *Rutilus rutilus, Perca fluviatilis,* and *Barbus barbus* are dominant; *Acipenser ruthenus* and the predatory

TABLE 1. Fish species mentioned in text.

	Danube		
	Upper	Middle	Lower
Acipenseridae			
Acipenser güldenstaedti (BRANDT)	—	?	+
Acipenser nudiventris (LOVETZKY)	—	?	?
Acipenser ruthenus L.	+	+	+
Acipenser stellatus (PALLAS)	—	—	+
Acipenser sturio L.	—	—	?
Huso huso L.	—	—	+
Clupeidae			
Alosa caspia tanaica (PAVLOV)	—	—	+
Alosa pontica (EICHWALD)	—	—	+
Clupeonella cultriventris (NORDMANN)	—	—	+
Salmonidae			
Hucho hucho L.	+	?	—
Salmo gairdneri (RICH.)	+	?	—
Salmo trutta f. fario L.	+	?	—
Salmo trutta labrax (PALLAS)	—	—	+
Salvelinus fontinalis (MITCHILL)	+	—	—
Coregonidae			
Coregonus lavaretus L.	—	?	—
Coregonus peled (GMEL.)	+	—	—
Thymallidae			
Thymallus thymallus L.	+	—	—
Esocidae			
Esox lucius L.	+	+	+
Cyprinidae			
Abramis ballerus L.	+	+	+
Abramis brama L.	+	+	+
Abramis sapa (PALLAS)	+	+	+
Alburnus alburnus L.	+	+	+
Aristichthys nobilis (RICH.)	+	+	+
Aspius aspius L.	+	+	+
Barbus barbus L.	+	+	+
Blicca björkna L.	+	+	+
Carassius auratus (L.) 1758	+	+	+
Carassius carassius (L.) 1758	+	+	+
Chondrostoma nasus L.	+	+	+
Ctenopharyngodon idella (VAL.)	+	+	+
Cyprinus carpio L.	+	+	+
Hypophthalmichthys molitrix (VAL.)	+	+	+
Leuciscus cephalus L.	+	+	+
Leuciscus idus L.	+	+	+
Pelecus cultratus L.	+	+	+
Pseudorashora parva (SCHLEGEL)	+	+	+
Rutilus rutilus L.	+	+	+
Scardinius erythrophthalmus L.	+	+	+
Tinca tinca L.	+	+	+
Vimba vimba L.	+	+	+
Catastomidae			
Ictiobus cyprinellus (VAL.)	?	+	+
Ictiobus bubalus (RAF.)	?	+	+
Ictiobus niger (RAF.)	?	+	+
Cobitidae			
Misgurnus fossilis L.	+	+	+
Siluridae			
Silurus glanis L.	+	+	+
Ictaluridae			
Ictalurus nebulosus (LE SUEUR)	—	+	—
Anguillidae			
Anguilla anguilla L.	+	+	+
Gasterosteidae			
Gasterosteus aculeatus L.	+	+	+
Syngnathidae			
Syngnathus nigrolineatus (EICHWALD)	—	—	+
Atherinidae			
Atherina boyeri pontica	—	—	+
Centrarchidae			
Lepomis gibbosus L.	+	+	+
Micropterus dolomieui (LACEPEDE)	+	—	—
Percidae			
Perca fluviatilis L.	+	+	+
Stizostedion lucioperca L.	+	+	+
Zingel streber (SIEBOLD)	+	+	+
Zingel zingel L.	+	+	+
Gobiidae			
Protherorhinus marmoratus (PALLAS)	+	+	+

Stizostedion lucioperca, Silurus glanis and *Esox lucius* are also found.

Lower Danube (942 km)

The upper subdivision is represented by the 80 km long Iron Gates II reservoir, where fish fauna are undergoing transformation caused by the 1984 barrage construction. The middle subdivision (over 700 km) reaches Galati. Before longitudinal dikes were constructed (1965–78), this subdivision was much richer in freshwater fish. Now small cyprinids, breams, *Perca fluviatilus, Stizostedion lucioperca* and *Silurus glanis* are the main species. Migratory sturgeons and Clupeidae also appear seasonally for reproduction. The lowest subdivision includes the main stream, arms, undammed pools and lakes of the delta. The freshwater species here are mostly small and medium-sized species, although *Silurus glanis, Stizostedion lucioperca, Aspius aspius* and rarely *Cyprinus carpio* are also fished as larger individuals. The main fishery for migrating species is also located here.

Euryhaline marine species of the families Clupeidae, Gasterosteidae, Syngnathidae, Atherinidae and Gobiidae enter the lower part of the delta. The Gobiidae in particular is represented by many species and plays an important trophic role (Banarescu 1957; Teodorescu-Leonte 1966).

The number of species increases from source to mouth: in the upper reaches 59 species are present; in the middle reaches 72 (although some are not confirmed) and in the lower reaches 73 (Bacalbaşa-Dobrovici et al. 1984).

There are three principal groupings of fish:

i) species living only in the river channel (*Acipenser ruthenus, Barbus barbus, Zingel streber, Z. zingel*);
ii) species living in the permanent waters of the floodplain and the inundated zones (*Tinca tinca, Carassius carassius, Misgurnus fossilis*, etc.), and
iii) semi-migratory species, feeding in the marine fringes of the delta, in the delta itself or in the lower reaches of the river and performing anadromous reproductive migrations. These same species are also present in the middle reaches of the Danube, but their migrations to the freshly flooded zones are shorter, e.g. *Cyprinus carpio, Leuciscus idus, Stizostedion lucioperca*, and

Silurus glanis.

Oxbow lakes offer favourable conditions for fish, especially when access to the main stem of the river is maintained throughout the year. River banks between reservoirs of the upper Danube are consolidated with rubble creating favourable conditions for some species (Janisch 1980). In the flowing sectors of Austrian reservoirs, benthic fauna are well developed, but the lack of zooplankton and spawning beds for most species has led to a decline of rheophilic and limnophilic fish populations (Jungwirth 1984). The importance of oxbow lakes as shelter for fishes in the middle Danube was emphasized by Holcík et al. (1981).

The distribution and movement of fish in the middle Danube was investigated by Janković (1971, 1974) and in the lower reaches by Antipa (1910, 1916), Banarescu (1964), Bacalbasa (1965), and Salnikov (1961). The distribution of fish in various floodplain habitats depends on water level, vegetation and the spawning and feeding requirements of adult fish, as well as numbers of fish remaining in floodplain pools from the previous year and the number of fish entering from channels. Fish avoid thick floodplain woods and compact reed growth, showing a preference for dispersed vegetation with aufwuchs for spawning and feeding. Predatory fish are also attracted to these habitats where prey congregate.

After spawning, adult fish tend to return to the channel with the first movement of water off the floodplains. Fish remaining in permanent pools and backwaters are intensely fished and in shallower waters are eaten by fish-eating birds or, during severe winters, die from anoxia. Fisheries on the floodplain are based mainly on Cyprinidae and Percidae.

In the maritime zone of the delta, changes in water level frequently associated with variations in salinity produce changes in the fish population. Fish enter or retire from the river or sea delta and foredelta. The penetration of freshwater species into the foredelta may be hazardous. For instance, *Stizostedion lucioperca* is somewhat adapted to brackish water, but cannot survive in a salinity exceeding 8 %, thus mortalities of the species follow after onshore winds produce rapid changes in salinity.

Migrations

In the upper and middle Danube, the most frequent migrations were local (*Chondrostoma nasus, Barbus barbus*, Salmonidae, etc.). In the nineteenth century, sturgeons (*Huso huso, Acipenser güldenstaedti* and *A. stellatus*) migrated, rarely, up to Bavaria (Terofal 1980). Before 1969 (Iron Gates I damming), *Alosa pontica* migrated in some years up to Novi Sad. Presently, the great migrations have stopped; the local ones are also reduced, owing to hydraulic changes and polluted tributaries.

For the lower Danube, including the delta, Antipa (1916) distinguished typical migrations and aperiodical movements, caused by deterioration of environmental conditions. Cyclical migrations of floodplain species consist of: (1) at the beginning of spring, fish leave floodplain lakes (now very rare) seeking higher O_2 concentrations; (2) during the spring flood, fish take refuge on the floodplain, to avoid currents and suspended matter; (3) from the deep floodplain lakes (now mainly from the river channel and the inundated floodplain), fish migrate to spawning places (also rare) on the floodplain margins; (4) in summer, fish leave the floodplain for the river, and (5) in autumn some species return to the floodplain lakes for overwintering (now only in some years and in small numbers).

In spring, some upstream reproductory migrations occur with semi-migratory delta species. During heavy floods, at the end of spring and the beginning of summer, delta fish move to the foredelta for feeding. Aperiodical migrations (compelled ones) consist of movements to avoid anoxic conditions and in response to changing salinities in the foredelta.

Migrations of typical migratory species are for spawning (migratory sturgeon and Clupeidae) and feeding (Mugilidae). Although migrations have remained basically the same, distances and intensities (with the exception of *Alosa pontica*) have been drastically reduced, especially for upstream delta migrations, where, instead of great quantities of *Cyprinus carpio*, there are smaller runs of *Carassius auratus*.

Human interventions, especially through the construction of barrages, have considerably shortened migratory pathways. Anadromous species from the Black Sea, (*Salmo trutta labrax, Alosa pontica* and sturgeon *Huso huso, Acipenser güldenstaedti* and *A. stellatus*) now spawn between Brăila and Ostrovul Mare. Black Sea shad were not affected by river works and, owing to some changes of the Black Sea fish fauna, quantities taken from 1974 surpassed the average of previous years. By contrast, the Danube sturgeon fishery has declined since the beginning of the Century. Peak migrations of *Huso huso* occur during February–April and September–November (two migratory forms) although spawning for both migrations takes place in April–June (Banarescu 1964). *Acipenser güldenstaedti* also has two migration peaks, February–May and August–October, and in some years may have a third. Spawning for all forms occurs in spring[1].

The migratory clupeid, *Alosa caspia tanaica* and *Alosa pontica* occur in the river in spring during the flood. Fry of the Black Sea shad drift downstream on the water surface. Maximum fry concentrations (55–64 % of individuals) occur in the middle of the river (Vladimirov 1953). The drift of fry formerly lasted 4 months, but that period is now very reduced. When fry reach the sea they are 60 mm or more in length and are dispersed throughout the foredelta (Lyashenko 1953). The smallest Danubian clupeid, *Clupeonella c. cultriventris*, ascend to 150 km up river and in some winters are fished in floodplain lakes (Bacalbasa 1968b).

In the lower Danube, transversal migrations across the floodplain (see Antipa 1916), are now restricted to the small island of Braila and the Delta system, which are not dammed. Even here migrations have been reduced, especially through a drastic reduction in numbers of semi-migratory fish from the delta. As a rule, fish penetrate the floodplain gradually, but leave as a group between June and September, when the water level drops by about 3.5 m in the Brăila zone and 3.0 m in the Prut-Isaccea zone. The rate of withdrawal of fish is directly proportional to the speed of retreating water.

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[1] After Manea (1980) there is also a non-migratory form of *Acipenser güldenstaedti*.

Information on the sequence of fish entry onto the floodplain is fragmentary and uncertain. It is known that *Aspius aspius* is the first species to move from the main channel to the floodplain and is followed closely by *Silurus glanis*. The order in which fish leave the floodplain has been better studied. *Aspius aspius* and larger individuals of *Silurus glanis* are the first to leave. These are followed by *Abramis brama, Blicca björkna, Abramis ballerus, A. sapa, Rutilus rutilus, Scardinius erythrophthalmus, Alburnus alburnus* and *Esox lucius*. *Leuciscus idus* and *Cyprinus carpio* are the last to abandon the floodplain for the main river channel.

There are some small euryhaline species, which enter the Danube more or less regularly. *Atherina boyeri pontica* penetrates lagoons of the delta while *Gasterosteus aculeatus* makes short forages up estuaries. Mullets, which formerly yielded catches of up to 400–600 t•yr^{-1} in the delta lagoons have now declined in importance.

Productivity

Standing Stock

The most important fisheries of the lower reaches of the Danube are in Romania. Here the shallow nature of the floodplain permitted estimates to be made of floodplain standing stocks (Antipa 1910). These estimates remain valid even now. The fishing coefficient for seines under various conditions was determined by Busnita (1957). Estimates were based on seine-net catches at the beginning and after closure of the lake fishery, providing enough data to derive estimates of standing stock. For instance, the standing stock of Bugeac Lake (river km 340) was 300 kg•ha^{-1} before the 1956 fishing season and 63.3 kg•ha^{-1} after the closure. The quantity of fish concentrated in the lake of a closed floodplain depression represents the whole production of the depression and cases have been recorded of total catches of between 2 000 and 3 000 kg•ha^{-1} in such waters. The fish production under unconstrained flood regimes depends on flood height, timing and duration, climatic conditions, especially during the spawning period, and the species structure of the community. The major subdivisions of the lower Danube floodplain produced an average production of 80–110 kg•ha^{-1}, although much higher values are on record.

Estimates of standing stock have been made in Czechoslovakia by Balon (1964) and Holcík et al. (1981). The fish population of the Zofin arm (river km 1836.3) was investigated by mark-and-recapture twice yearly. The density and composition of fish populations in the arm showed great variations in response to changes in hydrological regime. The average standing stock for the period 1969–73 was about 292 kg•ha^{-1} (4.04 kg × 100 m^{-3}) (Holcík and Bastl 1976). Annual available production of fish in the section of the Danube between the mouths of the Morava and Ipel rivers was estimated at 749 t, some 608 t of which were in the arms and 140 t in the main channel (Holcík et al. 1981). However, methods to determine standing stock in the main channels are less reliable.

Fishing Gear, Methods and Catch per Unit Effort

Sport fishing is dominant in West Germany, Switzerland, Austria, and Czechoslovakia, although commercial fishing is practiced in the upper Danube and its tributaries (Bruschek 1964; Janisch 1980). Only one small commercial fishing team was active in Czechoslovakia during 1985.

Commercial fisheries are more important in the middle and lower Danube. At the beginning of this Century, I. Ianko's "Origin of the Hungarian Fishery of 1910" and the monumental work of Antipa (1916) described the diversity of gear. Gear used in 1965 is summarized in Table 2, together with associated catch rates. As a consequence of modified ecological conditions in the lower Danube and the creation of the Iron Gates I reservoir, many of these methods are now disappearing and catch rates for most fishing gear have been reduced compared with 20 years ago.

Yield

In West Germany, upstream from Ulm, a yield of 65–76 kg•ha^{-1} is recorded, of which about 73 % represents good quality fish such as *Salmo trutta* f. *fario, Esox lucius, Thymallus thymallus*, and *Anguilla anguilla*. If species caught by the 400–500 sport fishermen were also included, the yield could be as high as 100 kg•ha^{-1} (Strubelt 1975). In Bavaria, during 1981, approximately 100 families of fishermen fished 132 t of Cyprinids, *Anguilla anguilla, Esox lucius* and salmonids (G. Keiz, Meisenweg lc, 8 011 Vaterstetten, West Germany, unpubl. data).

There are no reliable catch figures for Austrian waters. Liepolt (1972) reported a mean yield of 20 kg•km^{-1} of river equivalent to 1 734 t•yr^{-1}. Janisch (1980) estimated catches of 32 kg•ha^{-1} for the main channel of the Danube in the Abwinden–Asten zone and 45–120 kg•ha^{-1} for other associated fish producing waters.

Catches in the middle and lower Danube have remained relatively constant during the last few years, with a tendency for the proportion of migratory sturgeon, as well as *Tinca tinca, Cyprinus carpio*, and *Esox lucius* to diminish. Total fish yield from the undammed lower Danube is approximately half the yield obtained from the river prior to the changes by hydraulic works. However, this reduction has been partially offset by fish yield from relict floodplain lakes and intensive aquaculture in newly constructed ponds (Table 3). As well, fish quality has been affected, with *Cyprinus carpio* being supplanted by less desirable species (e.g. *Carassius auratus* and *Rutilus rutilus*). Data on fish catches from middle and lower Danube countries, between 1958 and 1983 (Table 4), show wide variation.

Fisheries Management Practices

Systematic management of the aquatic ecosystem for conservation is beginning in the upper Danube. In Austria as well as West Germany guidelines are available for the preservation of landscape and fish productivity from running waters (Leitfaden 1984). Although fisheries legislation differs amongst countries and even states, all have the same basic objective of protecting young fish and endangered species. In addition, maintenance stocking and the introduction of new species is widely used. In West Germany and Austria, *Salvelinus fontinalis, Salmo gairdneri* and *Coregonus* spp. have been introduced, mostly to tributaries. During the last few decades East Asian plant-eating Cyprinids have also been stocked. Populations of *Anguilla anguilla, Acipenser*

TABLE 2. Characteristics of the principal fishing methods in the lower Danube (Bacalbasa-Dobrovici 1965) and Iron Gates I Reservoir.

Gear	Method	Biotope	Catch rate	Present situation
CHANNEL FISHERY				
Visila	Baited setline for *Silurus glanis*	Steep banks	35 kg•yr^{-1}	Declining
Longline	Baited for *Cyprinus carpio*	Perpendicular to shallow banks	up to 200 kg•yr^{-1}	Almost disappeared
Small sheat-fish longline	Baited for *Silurus glanis*	Perpendicular to the river bank	150–400 kg•yr^{-1}	Declining
Sterlet longline	Baited for *Acipenser ruthenus*	On channel bottom	15–40 kg•yr^{-1}	Almost disappeared
Superficial longline	Baited for *Silurus glanis*	Fixed at the surface	up to 300 kg•yr^{-1}	Almost disappeared
Carmacs	Sturgeon longline with ripping hooks	Fixed on the channel bottom	30 kg•yr^{-1}	Prohibited
Carp trammel net	Drifted with additional traction for *Cyprinus carpio*	On the channel bottom	30–40 kg•d^{-1}	Maintained with less productivity for other fish
Sterlet trammel net	Bottom drift for *Acipenser ruthenus*	On the channel bottom in deep zones	60 kg•yr^{-1}	Almost disappeared
Black Sea shad trammel net	Drifting in the water mass for *Alosa pontica pontica*	Main channel, current zones	50–70 kg•d^{-1}	Currently in use
Trandadaia	Frame drifting with scaring trammel net	Bottom and bottom pits	400–800 kg•yr^{-1}	Almost disappeared
Trap net	Fixed at the mouth of St. George arm for *Clupeonella cultriventris*	Near the river bank	up to 800 kg•d^{-1}	Currently in use for a short seasonal fishery
Fyke net	During the migrations of freshwaters fishes by turbid water	Near the river banks in shallow water	up to 15–20 kg•d^{-1}	Declining
Tarabuf	Great mobile one-bag net with fish scaring device	Abrupt banks with tree roots	3 000–6 000 kg•yr^{-1}	Declining
Oria	One-boat drafted bag net for freshwater fish migration	Channel in different depths	30–40 kg•d^{-1}	Almost disappeared
Laptash	Two-boat trawled bag net for freshwater fish in cold water	Bottom and bottom pits	2 000–5 000 kg•yr^{-1}	Currently in use
Two-boat trawl	Trawling with the current	Channel bottom	up to 80 000 kg•yr^{-1}	Prohibited
Seine without bag	One wing at the bank, the other trawled with the current	Shallow banks	8 000–12 000 kg•yr^{-1}	Declining
River seine[a]	Mechanical traction with the current	3/4 of the river breadth	280 kg•d^{-1}	Disappeared as not economical
Electrical fishing[b]	Motor-boat with electrodes advancing slowly upstream	Abrupt banks with tree roots	up to 10 000 kg•mo^{-1}	Prohibited
FLOODPLAIN FISHERY				
Trammel nets	The fish is scared to net	Floodplain lakes	up to 200 kg•d^{-1}	Declining
Roach gillnets	Fixed nets for *Rutilus rutilus*	Floodplain lakes	up to 25 kg•d^{-1}	Declining
Pike-perch trammel net	Fixed net; also in winter under ice	Floodplain lakes	up to 300 kg•yr^{-1}	Declining
Barrage stow net	Fish is pushed by the current into the gear	Canals and arms	30 000–100 000 kg•yr^{-1}	Almost disappeared
Fyke net	Rows of gear in the way of feeding fish	Permanent and temporary lakes with vegetation	40–50 kg•yr^{-1}	Currently in use
Lake talian	Trap net with leader and 3 harvesting fyke nets	Mostly Delta lakes and arms	up to 600 kg•yr^{-1}	Currently in use
Zatoane	Big weirs (of reed) encircling wintering fish	Wintering places with emerged vegetation	up to 30 000 kg•yr^{-1}	Prohibited
Cotets	Winter fishing; row of small reed weirs with leaders	In the aquatic vegetation with winter fish movements	up to 6 000 kg•yr^{-1}	Almost disappeared
Vintroaie (great fyke net)	Near fences for *Silurus glanis*	Shallow arms and depressions during flood	100–150 kg•yr^{-1}	Currently in use
Cast net	To capture crowded fish	Fenced arms and canals	up to 600 kg•yr^{-1}	Declining
Lake seine[c]	Two-boat method, mostly associated to four-seine	Larger lakes	40 000 kg•yr^{-1}	Currently in use

TABLE 2. (cont'd) Characteristics of the principal fishing methods in the lower Danube (Bacalbasa-Dobrovici 1965) and Iron Gates I Reservoir.

Gear	Method	Biotope	Catch rate	Present situation
ZONE OF IRON GATES I SPECIFIC FISHERY				
Large metal basket[d]	Capturing fish swimming upstream	Banks with swift current	up to 1 000 $kg \cdot yr^{-1}$	Disappeared
Sakovishte[e,f]	Scoop net installed on special platform	Near banks with countercurrent	up to 3 000 $kg \cdot yr^{-1}$	Almost disappeared
Trammel nets [g]	Fixed, drive-in and/or drift	Weak or medium current zones	0.95–6.20 kg × 100 $m^{-2} \cdot d^{-1}$	Currently in use

[a] Bacalbasa-Dobrovici (1957).
[b] Bacalbasa-Dobrovici (1963).
[c] Bacalbasa-Dobrovici (1968a).
[d] Bacalbasa-Dobrovici (1971).
[e] FAO (1975).
[f] Bacalbasa-Dobrovici (1975).
[g] Bacalbasa and Petcu (1969b).

TABLE 3. Fish catch (tons) in the middle and lower Danube and its extensive aquaculture fish culture units during 1981 (FAO 1963).

Species or group of fish	Total	Czechoslovakia	Hungary	Yugoslavia	Bulgaria	Romania	USSR
Alosa pontica pontica	1 003.0	—	—	—	57.0	650.3	295.7
Cyprinus carpio	519.4	12.9	107.1[a]	158.2	6.9	230.4	3.9
Stizostedion lucioperca	615.1	6.2	16.9	101.2	8.5	478.1	4.2
Silurus glanis	558.3	1.7	5.7	105.7	8.7	427.6	8.9
Carassius auratus gibelio	3 159.9	—	—	119.3	8.5	2 806.9	225.2
Rutilus rutilus	1 988.6	—	—	—	—	1 988.6	—
Esox lucius	814.3	7.3	20.7	105.4	1.9	674.4	4.5
Cyprinids (plant and plankton-eating)	259.2	0.9	234.6[a]	9.9	1.7	11.6	0.5
Migratory sturgeon	101.8	—	—	13.6	14.6	69.3	14.3
Total (including other species)	13 279.7	119.0	900.7	1 088.1	478.1	10 057.7	654.1
Production from extensive aquaculture units	13 474.1	—	—	—	—	11 080.0	2 394.1
Total	26 771.8	119.0	900.7	1 088.1	478.1	21 137.7	3 048.2

[a] Probably includes some fish produced in extensive aquaculture units.

ruthenus, *Hucho hucho*, *Salmo trutta fario* and *Thymallus thymallus* are maintained by regular stocking.

In the middle and lower Danube, exploitation is rationalized through the recommendations of the Joint Commission for the Application of the Fishery Convention in the Danube.

Extensive aquaculture is practiced in the oxbows and lakes isolated by hydraulic works. Fry and young fish saved from shallow floodplain lakes liable to desiccation by the withdrawal of floodwaters are used for stocking. In Hungary, some waters are stocked with eels while East Asian plant-eating Cyprinids are used in all Danube countries. Stocking with pike-perch, pike and *Silurus glanis* is much less common.

In the lower Danube, engineering activities for fisheries related to hydraulic works are designed to mitigate adverse effects they might have on aquatic life. Programmes include pond construction on the former or present river floodplain. Fish passes have not yet been used in the lower Danube, but provisions should be made in the construction of future barrages for the passage of anadromous sturgeon and *Alosa pontica*. Many types of structures have also been installed to prevent fish from being drawn into irrigation systems or the Danube pumping station.

In Romania, there was also some stocking with the fry of *Acipenser ruthenus* and *A. güldenstaedti*, between 1956 and 1962. The Iron Gates I reservoir was stocked with *A. ruthenus* fry shortly after its construction (Manea 1980).

Lakes for irrigation and fisheries, or for fish rearing, exist both in the Romanian and the Soviet Union zones of the Danube. In Romania there are many pond farms on now bunded floodplain, the largest of which is in the delta. Such farms and hatcheries provide the bulk of the fish production (Table 5). During 1960–82, 46 650 ha of fish ponds were constructed in the Romanian part of the Danube delta.

In the Danube delta polyculture is dominant. the main species is *Cyprinus carpio*, with additional stocking of *Ctenopharyngodon idella*, *Hypophthalmichthys molitrix* and *Aristichthys nobilis*; in the last decennium 3 species of *Ictiobus*: (*I. cyprinellus*, *I. bubalus* and *I. niger*) were also introduced. East Asian zooplankton and plant-eating Cyprinids have contributed 24 % to the delta fish pond production in recent years (Nitu 1983). Fish-rearing in the delta has been difficult because of predation by fish-eating

TABLE 4. Data on fish catches of individual Danubian countries from 1958 to 1983 (Materially XXIV...1983).

Year	Czechoslovakia	Hungary	Yugoslavia	Bulgaria	Romania	USSR	Total
1958		755.4	1288.1	1064.8	28110.0	2696.5	33914.8
1959		812.5	1189.1	631.3	12920.6	1985.0	17538.4
1960		797.1	1071.1	408.1	9748.7	1026.5	13051.5
1961	174.4	839.9	1198.6	566.0	12300.0	1588.6	16667.5
1962	192.1	875.5	1195.5	980.6	18645.6	1566.5	23455.7
1963	191.0	893.4	1686.0	744.8	22042.3	2081.0	27638.5
1964	185.4	849.2	891.8	536.6	14639.0	2097.0	19199.0
1965	249.7	964.9	1707.2	1084.9	23024.0	1651.1	28681.8
1966	214.0	1194.5	2555.7	590.3	22308.0	2226.0	29118.5
1967	280.7	1141.6	2128.1	724.9	23500.0	2415.5	30190.9
1968	224.2	1077.9	1425.7	538.7	15499.9	1597.9	20364.3
1969	162.4	892.8	858.2	406.2	18783.2	1247.4	22350.3
1970	106.0	1007.6	1622.7	540.9	28182.7	2175.6	33585.5
1971	104.2	1083.3	1251.9	529.0	17300.0	2239.1	22507.4
1972	131.8	908.4	1070.8	508.5	20854.3	1760.2	25234.0
1973	156.8	883.3	1214.0	422.0	29573.0	1828.4	34077.5
1974	190.2	954.7	957.4	497.2	28455.2	2627.6	33682.2
1975	173.2	1018.4	1112.3	577.5	30472.0	3129.8	36483.2
1976	235.3	1067.5	1030.7	455.3	28879.0	2834.8	34502.6
1977	206.7	972.0	1025.2	385.6	31829.9	2919.0	37338.4
1978	147.7	939.5	1052.6	479.0	18384.4	2973.7	23976.8
1979	168.1	925.3	1009.4	464.7	19146.5	3295.8	25009.8
1980	154.2	807.1	939.0	435.0	17711.0	3100.3	23146.7
1981	119.0	900.7	1088.1	478.1	21079.7	3049.0	26714.6
1982	131.0	912.5	931.0	466.6	11824.8[a]	2879.0	17144.8
1983	152.8	823.7	955.5	423.5	8991.3[a]	2951.9	14298.8

[a] Only for the Danube.

TABLE 5. Romanian Danube delta fish pond construction (Nitu 1983).

Category	Surface (ha)	Average production (kg•ha^{-1})
Hatcheries	5 230	968
Fish farms	18 890	1 220
Idem with extensive exploitation	22 530	357

birds (Pasculescu et al. 1962), but some remedies have been suggested (Bacalbasa 1979).

The highest Soviet Union delta fish production comes from dammed lakes. They now are beginning to produce in the same way that Lake Sasik (20 000 ha) was transformed by supplying the lake with fresh water.

Conclusion

The present Danube River fisheries are fundamentally different from those at the beginning of the Century. The river now has only the remnants of its extensive floodplain, barrages have cut the Danube into many long sections with or without tributaries, and a great number of tributaries are polluted. In the middle and especially the lower Danube, great quantities of water are pumped for irrigation, and the channel is heavily navigated. Many oxbows are completely, or at least at low water level, isolated from the river. The delta is partially transformed through longitudinal dikes in agricultural land and in such conditions many fish species are decreasing with the floodplain-bound species and sturgeons being first.

To maintain the Danube fisheries, a great deal of research must be done in order to advise governments of the necessity for ecologically founded hydraulic conditions. The river exploitation of other economically important branches should also be managed to minimize harm to the open river fisheries — the Cinderella of most great river economies.

At the same time, active human intervention is maintaining fish production in the recently deteriorated open-river conditions. In the upper Danube, stocking and the beginning of ecologically influenced hydraulics and land construction are taking place. In the middle river, there is a lesser degree of stocking and an intense aquacultural oxbow exploitation (Hungary). In the lower Danube, especially in delta reaches, an extensive fish-rearing program has been developed in specially constructed farms (Romania) and in lakes (USSR and Romania).

The Romanian program for the amelioration and exploitation of the Danube delta provides for the continuation of construction of ponds and other engineering works to cover an area of 63 000 ha with a potential fish yield of 77 000 t•yr^{-1} (Stanuca 1983). Beginning in 1988, the Razelm Complex (76 000 ha) will also be exploited by stocking.

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References

Antipa, G. 1910. Regiunea inundabila a Dunarii. C. Gobl. Bucuresti. 318 p.

1911. Fisherei und Flussregulierung. Allgemeine Fischerei-Zeitung. 16 und 17: 8 p. (Sonder-Abdruck).

1916. Pescaria si pescuitul in România. Academia Romāna, Bucuresti, Fond. V. Adamachi, 8(46): 794 p.

1935. L'organisation générale de la vie collective et du mécanisme de la production dans la biosphère. Academie Roumaine, Bucarest, Études et recherches VI: 84 p.

Bacalbaşa, N. 1957. Pescuitul cu navodul fluvial în Dunare. Industria Alimentara, Bucuresti 8–9; 8–11.

1963. Pescuitul cu ajutorul curentului electric. Industria Alimentara, Bucuresti 12: 522–526.

1965. Tehnica pescuitului (Pescuitul industrial). Editura Didactica si Pedagogica, Bucuresti. 680 p.

Bacalbaşa-Dobrovici, N. 1966. Cu privire la posibilitatile de crestere extensiva si de exploatare a broastelor comestibile în România. Industria Alimentara, Bucuresti 17(9): 484–486.

1968a. Quelques relations entre la limnologie et la technique de la pêche dans la région du bas Danube. Hidrobiologia 9: 245–253.

1968b. Die Fischereitechnik im Brates-See als Typus für die Donauseenfischerei. Colloquim Decennale Danubium, Varna, Bulgarien: 435–444.

1971. Eigentumliche Fischereimethoden mit Stazionärgeräten vom rumanischen Ufer des neuen Donaustausees "Eisernes Tor". Protokolle z. Fischereitechnik, Hamburg 12(58): 401–407.

1975. Efficacité des prises aux engins maillants dans le lac de barrage "Portes de Fer" et la sélection du poisson en fonction du maillage. Doc. techn. de la CECPI No. 23, Suppl. 1, Vol. I: 122–135, FAO, Rome.

1978. Die Benutzung von quantitativen Indikatoren fur die Ausnutzung der Fischerei von Zentralflusszonen, in deren Hochwasser-und Flussbett Wasserbautechnische Arbeiten ausgeführt worden. Bulet. Universit. Galati, An. I, Fasc. VII Techn. piscic., Galati: 25–35.

1979. La protection des oiseaux aquatiques et la pisciculture dans le Delta du Danube. Bulet. Universit. Galati, An. II, Fasc. VII Techn. piscic., Galati: 19–28.

1980. Influenta utilizarii economice a apei fluviilor asupra biotopilor si biocenozelor. Pontus Euxinus, Studii si cercet., I, Complexul muzeal de stiinte ale naturii, Constanta: 321–324.

1982. Anthropogene Einwirkungen auf Fischbestände. Schweiz. Z. Hydrol. 44(2): 243–251.

Bacalbaşa, N., and A. Petcu. 1969a. Over the fishery in the Romanian Danube sector in the reaches of Turnu Severin-Braziash. (Russian). Limnologische Donauforschungen. Berichte der XI. Konferenz z. Limnologie der Donau, IX 1967, Kiew, Naukova dumka, Kiev: 394–399.

1969b. Pescuitul cu sacovistea in zona viitorului lac de acumulare de la Portile de Fier. Hidrobiologia, Bucuresti; 10: 151–161.

Bacalbaşa-Dobrovici, N., P. Banarescu, J. Holcík, R. Janisch, D. Janković, G. Keiz, and E. Weber. 1984. Das Vorkommen einzelner Fischarten im Donaustrom und Uberschwemmungsgebiet im Jahre 1983 (Vorläufige Mitteilung). Wissenschaftliche Kurzreferate. 24. Arbeitstagung der Internat. Arbeitsgemeinschaft Donauforschung, Szentendre/Ungarn. Band II: 149–156.

Balon, E. 1964. Verzeichnis, Arten und quantitative Zusammensetzung der Ichthyofauna des Längs- und Querprofils des tschechoslowakischen Donauabschnittes. Zoologischer Anzeiger, Leipzig, 172(2): 113–130.

Banu, A. C. (coord.). 1967. Limnologia sectorului românesc al Dunarii. Edit. Acad. R.S.R., Bucuresti. 651 p.

Bacescu, M. 1967. Grigore Antipa (1867-1944). Anniversaires de l'UNESCO. Commission nationale de la R.S. de Roumanie pour l'UNESCO. 32 p.

Banarescu, P. 1957. Raspindirea si rolul biologic al guvizilor din Complexul Razelm. Bulet. Instit. Cercet. Piscicole. 16(2): 36–45.

1964. Pisces-Osteichthyes. Fauna R.P.R. XIII. Acad. R.P.R., Bucuresti. 962 p.

Breier, A. 1979. Modificari hidrografice recente în Delta Dunarii. Hidrotehnica, Bucuresti; XXIV: 247–252.

Brodskij, S. 1982. Uber die Krebsenfauna der unteren Donauläufen und Klassifikationsfragen der Familie Astacidae. XX. Internat. Tagung, Arbeitsgemeinschaft Donauforschung, Kiew. Naukova dumka: 223–227.

Bruschek, E. 1964. Elektrofischerei und Gewässerleitvermogen in Österreich. Österreichs Fischerei 3(4): 69–77.

Busnita, A. 1957. Prognoza productiei piscicole pe anul 1957 in regiunea inundabila si Delta Dunarii. Bulet. Instit. Certcet. Piscicole 16(3): 19–30.

Djisalov, N., and J. Tóth. 1978–1979. Development of stock of major predatory fish species on the Pannonian basin Hungaro-Yugoslav sector of the Danube. Annales Universit. Scient. Budapestiensis de Rolando Eötvös nominatae; T. XX-XXXI, Sectio Biologica: 261–264.

FAO Catalogue of Small Scale Fishing Gear. Edited by C. Nédélec. 1975. Fishing News (Books) Ltd. 191 p.

Gawrischowa, N. A. 1982. Bakterioplankton als Merkmal der Eutrophierung des Sowjetischen Donauabschnitts. XX. Internat. Tagung, Arbeitsgemeinschaft Donauforschung, Kiew. Naukova dumka: 129–131.

Giurescu, C. 1964. Istoria pescuitului si a pisciculturii în Romînia. Editura Academiei R.P.R., Bucuresti. 380 p.

Herzig, A. 1984. Zur Limnologie von Laufstauen alpiner Flüsse — Die Donau in Österreich. Oesterreischische Wasserwirtschaft 36(5/6): 95–103.

Holčík, J., and I. Bastl. 1976. Ecological effects of water level fluctuation upon the fish populations in the Danube River floodplain in Čzechoslovakia. Acta scientiarum naturalium Acad. Scient. Bohemoslovace Brno, X, Nova ser. 9, Praha. 48 p.

Holčík, J., I. Bastl, M. Ertl, and M. Vranovsky. 1981. Hydrobiology and ichthyology of the Čzechosolovak Danube in relation to predicted changes after the construction of the Gabcikovo-Nagymaros river barrage system. Prace labor.rybarstva a hydrobiologie, 3: 19–158.

Ivanov, K. 1982. Über chemische und termische Belastungen der Donau und ihrer Nebenflüsse. Schweiz. Z. Hydrol. Internat. Arbeitsgemeinschaft Donauforschung, 22. Arbeitstagung Basel 44(2): 181–193.

Janisch, R. 1980. Ergebnisse der Fischereilichen Beweissicherung im Zusammenhang mit der Errichtung des Donaukraftwerkes Abwinden-Asten. Naturkundliches Jahrbuch der Stadt Linz. 26: 31–102.

Janković, D. 1971. Die Erforschung de Aaltwässer und Überschwemmungsgebiete der Donau. Schweiz. Z. Hydrol. 33(1): 354–362.

1974. Untersuchungen des Djerdap-Strausses in den ersten Jahren nach seiner Bildung. Arbeitsgemeinschaft Donauforschung 16. Arbeitstagung in der CSSR, Bratislava. II: 76–85.

Jungwirth, M. 1984. Die Fischereilichen Verhältnisse in Laufstauen alpiner Flüsse, aufgezeigt am Beispiel der österreichischen Donau. Oesterreichische Wasserwirtschaft 36(5–6): 103–111.

Klokow, W. M. 1982. Zur Frage der Dynamik der höheren Wasserpflanzen im Kiliadelta der Donau. XX. Internat. Tagung, Arbeitsgemeinschaft Donauforschung, Kiew. Naukova dumka: 176–179.

Leitfaden Für Natur-und Landschaftsbezogenen Schutzwasserbau an Fliesgewässern. 1984. ÖWWV — Regelblatt 301. Bohmann Druck und Verlag, Wien. 151 p.

Leonte, V., and R. Teodorescu-Leonte. 1965. Cercetari hidrobiologice si ihtiologie pe bratul Sf. Gheorghe Bulet. Instit. Cercet. Piscicole: 24(3-4): 49–58.

Liepolt, R. 1972. Die Fischerei in Österreich. Oesterreichische Wasserwirtschaft, 24(9/10): 180–183.

Lyashenko, A. F. 1953. Juvenile Black Sea shad biology and their quantification, (Russian), p. 85–229. *In* Black Sea shad and the biological basis of their fishery. Akademiya nauk Ukrainskoj SSR, Kiev. Trudy Instituta Gidrobiologii, 28.

Manea, Gh. 1980. Sturionii. Edit. Ceres, Bucuresti. 244 p.

Marcoci, S., and V. Cure. 1981. Die Dynamik der saproben Struktur des Planktons im rumanischen Donauabschnitt. 22. Arbeitstagung, Basel. Internat. Arbeitstagung, Basel. Internat. Arbeitsgemeinschaft Donauforschung: 209–211.

Materialy XXIV Sessii Smeshannoj Komissii Po Primeneniju Soglashenya o Rybolovstve v Vodakh Dunaya. 1983. (Tezisy Dokladov i Soobschchenij), Moskva.

Matonickin, I., Z. Pavletić, and I. Munjko. 1975. Abiotische Aspekte des Ökosystems der unteren Save. Int. Arbeitsgem. Donauforschung, 18. Arbeitstagung, Regensburg, 18, 1. Teil: 23–29.

Mirica, Gh. 1956. Procesele de evolutie naturala si stadiul actual al Deltei Dunarii. Bulet. Institut. Cercet. Piscicole; 15(4): 9–18.

Miron, I. [ed.]. 1983. Lacul de acumulare Izvorul Muntelui-Bicaz. Edit. Acad. R.S.R., Bucuresti. 244 p.

Mociornita, C. 1958. Hidrologia in cadrul planului de amemajare a Deltei Dunarii. Hidrobiologia, 1, Edit. Acad. R.S.R.: 283–290.

Mogiltschenko, W. I., and P. G. Suchojwan. 1985. Ein Neuer Typ der Formierung von Ichthyofauna und Fischereiergiebigkeit des Gewassers am Beispiel des Sassyk-Stausees, der mit Donauwasser gespeist wird. 25. Arbeitstagung der Internat. Arbeitsgemeinschaft Donauforschung, Bratislava-CSSR: 385–388.

Munteanu, I. 1984. Die Evolution einiger trophischen Stufen für die Ichthyofauna in einigen Zonen des Donaudeltas und Razelmsees in der Periode 1982-1983. 24. Arbeitstagung der I.A.D., Szentendre-Ungarn. Band II: 161–164.

Naidenov, W., and D. Saiz. 1975. der Eifluss des regulierten Abflusses auf das Plankton der oberen Donau. 18. Arbeitstagung der I.A.D., Regensburg — W. Germany. 1. Teil: 239–243.

Nicolescu, D. 1982. Die Bakterien — ein Ausdruck der Tendenz der Selbstreinigung der Donau în der Zone des Stausees "Eisernes Tor". XX. Internat. Tagung der Arbeitsgemeinschaft Donauforschung, Kiew. Naukova dumka: 143–144.

Nitu, M. 1983. Coordonate ale activitatilor de pescuit si piscicultura din Delta Dunarii. Revista Economica, Bucuresti, 39: 5–6 si 40: 6–7.

Pasculescu, I., Gh. Machedon, and M. Ionescu. 1962. Nota privind actiunea daunatoare a pasazilor ihtiofage la pepiniera piscicola Sarinasuf. Bulet. Instit. Cercet. Piscicole; 21(3): 92–95.

Petran, M., and P. Kothé. 1975. Zusammenhange zwischen Geschiebetrieb und Benthos in Fliessgewässern. 18. Arbeitstagung der I.A.D., Regensburg — W. Germany. 1. Teil: 153–162.

Roman, T., L. Roman, and E. Lisandru. 1982. Das trophische Potential der Bodenarten des Donaudeltas und die Jahreszeitvariazionen der Hauptnahrungsstoffe Stickstoff, Phosphor, Kalium. 23. Arbeitstagung der I.A.D., Wien. Wissenschaftliche Kurzreferate: 27–29.

Romanenko, V. D., O. P. Oksiyuk, V. N. Zhukinskyj, and Yu. P. Shelyagsosonko. 1980. About the ecological fundamentation of the creation of the water-economical complex Danube-Dnieper. (Russian). Hydrob. Journ., XVI(5), Kiev: 3–12.

Romanenko, V. D., A. I. Iwanow, and L. L. Pyl. 1982. Bericht über die Phytoplanktonbesonderheiten im Kiliaarm der Donau im Jahre 1981. 23. Arbeitstagung der I.A.D., Wien. Wissenschaftliche Kurzreferate: 93–95.

Rojhdestvensky, A. 1968. Chemischer und Schwebstoffabfluss der Donau im Schwarzen Meer. Colloquium Decennale Danubium, Varna, Bulgarien: 93–102.

1979. Hydrochemical peculiarities of the lower Danube during 1975 (after observations in the Russe and Reni sectors) and their reflections in the Black Sea. XIX. Jubileumstagung der I.A.D., 26 IX–2 X 1976: 81–86.

Russev, B. 1981. Bulgarien, p. 53–60. *In* Internationale Arbeitsgemeinschaft Donauforschung der Societas Internationalis Limnologiae 25 Jahre.

1982. Eifluss der Stauanlagen auf die Entwicklung des Zoobenthos im österreichischen Donauabschnitt. 23. Arbeitstagung der I.A.D., Wien. Wissenschaftliche Kurzreferate: 139–141.

Salnikov, N. 1961. Fish Marking in the Lower Danube. (Russian). Joint Commission for the Application of the Fishery Convention in the Danube. Edit. of the Academy of Science of the Ukrainian SSR. Bul. 1: 45–49.

Spataru, A. 1979. Beaches and erosion processes. (in Romanian). Hidrotechnica, Bucuresti; XXIV: 51–54.

Stanojević, M. 1982. Physikalisch-chemische Eigenschaften des Donauwassers in SAP Vojvodina. XX. Internat. Tagung der Arbeitsgemeinschaft Donauforchung, Kiew. Naukova dumka: 63–66.

Stanuca, V. 1983. The Danube Delta in the future. Scînteia, 18 May (in Romanian).

Strahler, A. N. 1969. Physical geography, 3rd ed. J. Wiley and Sons, Inc. New York, NY. 596 p.

Strainer, M., K. Diaconu, and M. Bradatan. 1982. Dynamik einiger chemischer Indikatoren, erforscht im Wasser des Donaustromes. 23. Arbeitstagung der I.A.D., Wien. Wisseschaftliche Kurzreferate: 21–23.

Strubelt, T. 1975. Die Fischerei in der Donau zwischen Ulm und der Schleife bei Fridingen. 18. Arbeitstagung der I.A.D., Regensburg — W. Germany. 1. Teil: 385–387.

Terofal, F. 1980. Ausgestorbene und seltene Fische sowie Neueinburgerung in bayrische Gewasser. *In* Im Dienste der bayrishen Fischerei. Landesfischereiverband Bayern e.v., Munchen: 104–131.

Teodorescu-Leonte, R. 1966. Resultatele cercetarii bazei trofice a Razelmului si perspectivele productiei piscicole din acest complex prin dirijarea populatiei. Bulet. Instit. Cercet. Proiect. Piscicole; 25(1): 38–46.

Torke, W. 1985. Zur Fischfauna der Oberen Donau. Veröff. Naturschutz Landschaftspflege Bad.-Würt.: 323–343, Karlsruhe.

Tóth, J. 1983. About some predictable ecological problems and environmental impacts of the Bös (Gabčikovo) — Nagymaros barrage system. Földrajzi közlemények. XXXI (CVII) 1: 1–11.

Vidrascu, I. 1921. Volarificarea regiunii inundabile a Dunarii. Tip. "Urbana", Bucuresti. 370 p.

Vladimirov, V. I. 1953. Biology and survival of Black Sea shad larvae, (in Russian). *In* Black Sea shad and the biological basis of their fishery. Akad. nauk Ukrainskoj SSR, Kiev, Trudy Instituta Gidrobiologii; nr. 28: 30–66.

Weber, E., M. Jankovic, and G. Brezeanu. 1974. Limnologische Untersuchungen in tauräumendonaustaue. Arbeitsgemeinschaft Donauforschung 16. Arbeitstagung in der CSSR, Bratislava. II: 65–69.

Yearbook of Fishery Statistics. 1983. 56: 394 p. Rome, FAO.

ZINEVICI, V. 1982. Die Bildung und Entwicklung der Benthosfauna des Stausees "Eisernes Tor". XX. Internat. Tagung der Arbeitsgemeinschaft Donauforschung, Kiew. Naukova dumka: 216–218.

APPENDIX 1. Distances (km) from Sulina (Black Sea) of geographical objectives mentioned.

Name	Distance (km)	Name	Distance (km)
Apatin	1 404	Kilia Arm	0–115
Argesh River (*R.*)	431	Mohács	1 446.8
Baziash	1 072	Morava R.	1 884
Bratislava	1 872	Nagymaros	1 700
Budapest	1 646.5	Novi Sad	1 255
Danube-Black Sea Canal	300	Olt R.	600
Danube-Main-Rhine Canal	2 420	Paks	1 540
Danube-Tisza-Danube Canal	1 426	Prut R.	72[a]
Drava R.	1 387	Regensburg	2 379
Drobeta-Turnu Severin	931	Russe	495
Gabcikovo	1 820	Sava R.	1 175
Galati	150	Siret R.	155.5
Inn R.	2 230	South Morava R.	1 109
Ipel R.	1 714	Sulina	0
Iron Gates I barrage	942.5	Sulina Arm	0–34[a]
Iron Gates II barrage	862	Tisza R.	1 220
Isaccea	55[a]	Ulm	2 593
Ismail Ceatal	43[a]	Vienna	1 933
Kelheim	2 419	Zemun	1 174

[a] Distance in nautical miles (n.m.).

The Rhine River and Some of its Tributaries Under Human Impact in the Last Two Centuries

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Abstract

LELEK, A. 1989. The Rhine River and some of its tributaries under human impact in the last two centuries, p. 469-487. *In* D.P. Dodge [ed.] Proccedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The Rhine River has undergone dramatic changes in the last two centuries. Formerly a wild, salmon-rich stream the Rhine is now a ship chanal, with much of its floodplain almost disappeared. Man-made alterations to the stream, including heavy pollution, peaked in the 70's and almost caused the collapse of the fishery.

Former fish fauna included 44 species by the end of the last century. Additionally at least 17 non-native species have been introduced. Changes in the occurrence of fish species were studied qualitatively only, because data were not available to assess the changes quantitatively. A sequence of changes was constructed by grouping species and their occurrence into four categories: common, rare, sporadic and not recorded. Between 1890 and 1950, at least 27 taxa have declined in occurrence. This trend persisted between 1951 and 1975 when another 17 taxa were grouped lower. Since 1976, however, the decreasing trend was noticed in only two cases, for *Carassius carassius* and the feral form of *Cyprinus carpio*. Also, during the same period, 18 taxa were regrouped into the higher categories. This change was a consequence of the general improvement of water quality in the main watercourse itself, and in many tributaries including the formerly most polluted Main River.

Recent changes in water quality and the beginning of a recovery of the fishery are bases for modest optimism with respect to fishery management of the river. Plans and proposals have been developed for extension, recovery, and rehabilitation of the floodplains for a variety of purposes including general conservation and the fishery.

Résumé

LELEK, A. 1989. The Rhine River and some of its tributaries under human impact in the last two centuries, p. 469-487. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Le Rhin a subi des modifications spectaculaires au cours des deux derniers siècles. Anciennement un cours d'eau sauvage débordant de saumons, le Rhin est maintenant un canal de navigation dont la plus grande partie de la plaine d'inondation a disparu. Les changements apportés par l'homme à ce cours d'eau, y compris la pollution considérable, ont culminé pendant les années 1970 et ont presque entraîné l'effondrement de la pêche.

À la fin du dernier siècle, la faune piscicole comprenait 44 espèces en plus d'au moins 17 autres espèces exotiques introduites. Seules des études qualitatives ont été effectuées sur les variations de la présence des espèces de poissons étant donné qu'on ne disposait pas de données pour évaluer les variations quantitatives. On a déterminé une séquence des variations en groupant les espèces et leur présence en quatre catégories: commune, rare, sporadique et non signalée. De 1890 à 1950, l'abondance d'au moins 27 taxons abaissé. Cette tendance s'est poursuivie de 1951 à 1975: ainsi, 17 autres taxons ont été classés à un niveau inférieur. Depuis 1976, cette tendance à la baisse n'a été observée que dans deux cas, soit chez *Carassius carassius* et la forme sauvage de *Cyprinus carpio*. Pendant la même période, 18 taxons ont été classés dans des catégories supérieures. Ce changement est le résultat d'une amélioration générale de la qualité de l'eau dans de nombreux tributaires et dans le cours d'eau principal, y compris la rivière Main qui était la plus polluée.

Les changements récents de la qualité de l'eau et le rétablissement amorcé de la pêche laissent entrevoir un certain optimisme pour ce qui est de la gestion des pêches. On a établi des plans et des propositions pour l'expansion, le rétablissement et la réhabilitation des plaines d'inondation à diverses fins d'utilisation, y compris la conservation générale et la pêche.

Introduction

In the past 200 years hardly any other watercourse has undergone as many changes as the Rhine. Formerly a wild salmon stream, meandering through a bright floodplain, the river has since been transformed to a fully navigable ship canal. The river continues to link the Alps with the North Sea, and to supply 40 million people with water. A most complicated agglomeration of industry is located on its shores and main tributaries. Behind the veneer of passing water masses many chapters of European history are hidden, both good and creative as well as tragic. The most recent tragedy — the danger of ecological devastation — reached its peak in the 60's and 70's.

In the 80's things have changed for the better, not because of the physical quality of the stream itself but rather because of improvements in the fish fauna and fishery.

The latest setback in the recovery trend of the Rhine came unexpectedly. In the Swiss city of Basel (Bale), on November 1, 1986, a fire occurred in the Sandoz chemical warehouse, located on the shore of the river. The fire was brought under control, but water used to extinguish the fire flowed directly into the Rhine contaminating the river with pesticides, herbicides and fungicides. Currently, damages to the fauna are being evaluated. Preliminary results showed substantial losses of whole groups of invertebrates. Also the bottom-dwelling eel, *Anguilla anguilla* was wiped out for a stretch of about 300 km. As well, the contaminants may have a severe negative impact on the microbial activity necessary for the self-purification process, and also affect the fishery in years to come.

Although it is premature to assess the future for the recovery of the Rhine, particularly the timing of this process, optimism must be maintained. No doubt, increased research in limnology and in ecology of fish is needed now. A frenetic and spontaneous effort to stock the Rhine with eels is under way; however, the inordinately large numbers of eels being released may distort further the already unbalanced fish community.

I hope that this latest disaster may help to create a joint European committee to inventory damages, to predict future development and to advise fishery managers about long-term management for the Rhine.

Hydrography

The Rhine River, from its source in the Alps to the North Sea, is 1 320 km long and drains an area of 220 000 km^2. Its primary sources are located at 2344 m (Lake Toma) and at 2216 m (Paradis Glacier) in Switzerland. The two headwaters join at an elevation of about 660 m, to form the "Alpine Rhine" (Alpenrhein) which flows into Lake Constance (Bodensee). In the catchment of the Alpine Rhine 38 man-made barriers modify the water flow. The characteristics of the Alpine Rhine (Fig. 1, No. 1) are a high slope and heavy erosion. Despite 11 reservoirs on the main watercourse and others built on its tributaries, heavy sedimentation still occurs in the Alpine Rhine at its confluence with Lake Constance.

Lake Constance is of glacial origin with a lacustrine, formerly oligotrophic, environment, now showing patterns of eutrophication (see Elster and Einsele 1938; Elster 1974). Changes affecting fish taxa and fisheries are summarized by Toivonen (1972) and Hartmann and Nümann (1977). The lacustrine fauna include some glacial relicts, e.g. *Salvelinus alpinus* and coregonines, as well as species typical for the Danube catchment area, e.g. *Silurus glanis*. The importance of Lake Constance (surface area 539 km^2, volume 48.530 10^6 m^3, mean depth 100 m, max. depth 252 m) is its compensation of the Rhine River discharge which flows out of it. The water level of the lake itself fluctuates about 2 m. The increasing nutrient load of the former oligotrophic lake may have some impact on the fauna of the outlet stream, the "High Rhine" (Hochrhein), (Fig. 2, No. 2) but no observations of this impact on fish have been reported. The proliferation of underwater plants, particularly *Ranunculus fluitans* within the High Rhine (Thomas 1975), is attributed to increased levels of suspended nutrients.

The stream which begins as the outflow from Lake Constance, ie. as the "High Rhine", (Fig. 1, No. 2) is what is generally referred to as the Rhine. This part has a mean discharge of 232 m^3 s^{-1} which increases rapidly downstream due to the rich water supply of Alpine tributaries, particularly the Aare River, which contributes 564 m^3 s^{-1} to the flow. The water of this swiftly flowing river stretch has been used for power generation since the beginning of this century (Rheinfelden since 1898). At present, 11 dams generate electrical energy: see Stambach (1975) for further hydrological and energy information. This stretch is navigable only in its lower part up to km 151 (Rheinfelden).

The next river stretch, called the "Upper Rhine" (Oberrhein), (Fig. 1, No. 3) starting below the city of Basel (approx. km 170), was the most diversified part of the Rhine in the past. High water and floods created diverse stream bed formations resulting in a braided channel. Further downstream, nutrient-rich side waters formed and the vegetation developed concommitant with the diversification of the channel and the sequence of floods. Swift stretches extended over a length of about 190 stream km. (A reproduction of an old painting exemplifying this situation is presented in Fig. 2) This part of the Rhine is also known as the "furcation zone". Further downstream the valley broadened, sedimentation of suspended materials and inorganic drift occurred, the velocity of the current lessened, and the first meanders appeared (at about riverine 400 - 500 km). The "Upper Rhine" stretch has also undergone dramatic man-made changes beginning 170 years ago.

Field work on the modification of the river started in the mid - 19th century (1817 to 1876) following the ideas of Tulla ("Tulla's Rhine Rectification"). His aim was to confine the stream to one main channel the depth of which should maintain itself automatically. This goal was achieved and the concentrated water currents increased bottom scouring to a depth of 7 m in the proximity of 170–180 km (Basel). Slightly less erosion was recorded further downstream, extending 150–200 km down the river (below the city of Mannheim). Both the deepening of the stream channel and erosion of the loops of river bends damaged the classical unity of the stream and its valley. Many of the backwaters ceased to exist, the groundwater level dropped all along the stream and changes in the vegetation followed. For this giant project, performed virtually "by hand", Kunze (1982) provides quantitative data: construction of 250 km of high water embankments along both sides of the Rhine (about 5 × 10^6 m^3 of material) as well as about 200 km of different groins (consumption of 4 × 10^6 m^3 boulders and shot-rock). Both Kunze (1982) and Schäfer (1973) provide a detailed account of changes, the latter giving suggestions on how to mitigate some negative hydrological — and consequently ecological — changes. At present the slope of the river bed varies considerably and the veloc-

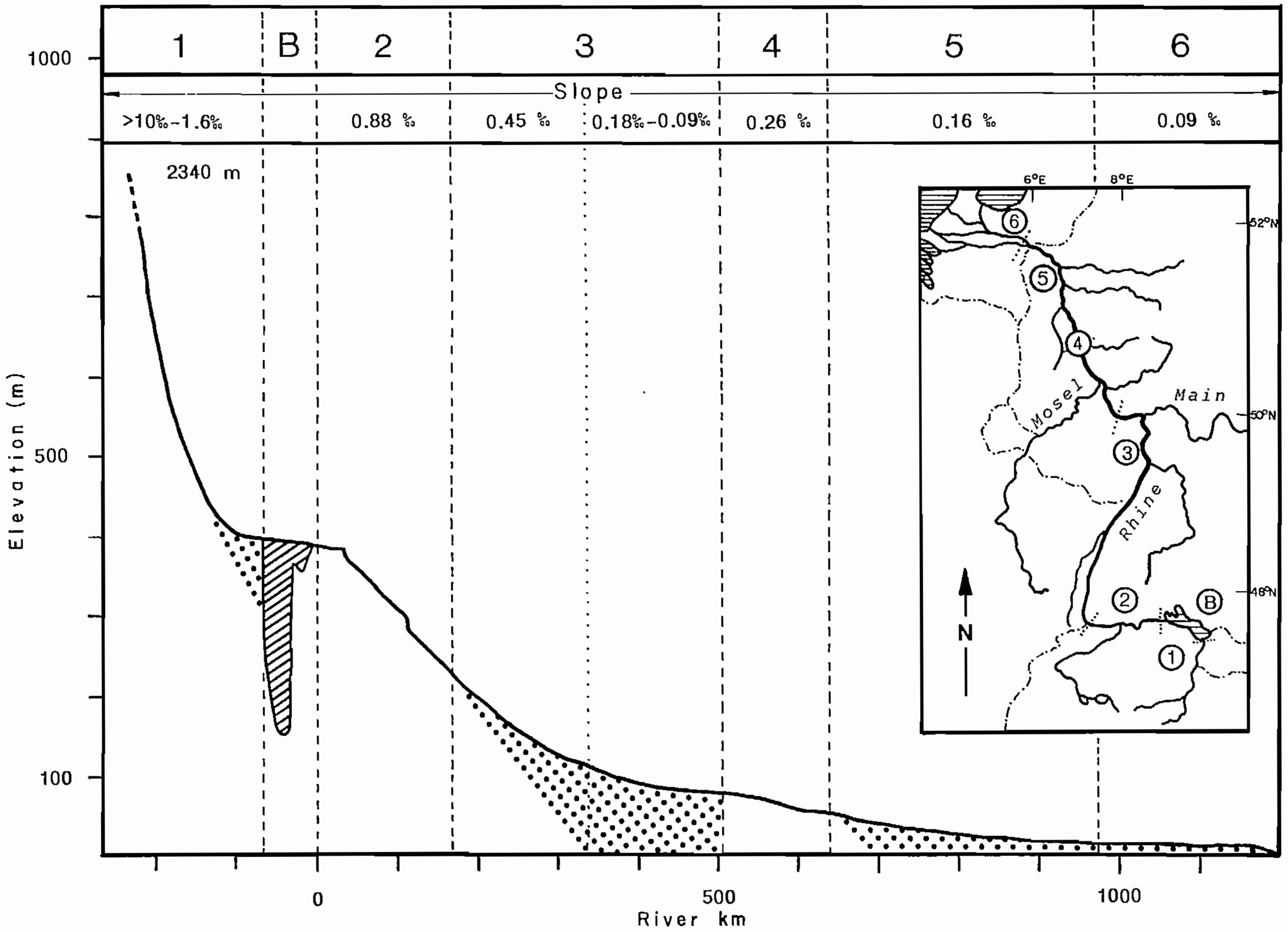

FIG. 1. A vertical profile of the Rhine River and its location (49°N, 8°E). 1 — Alpine Rhine (Alpenrhein); 2 — High Rhine (Hochrhein); 3 — Upper Rhine (Oberrhein); 4 — Middle Rhine (Mittelrhein); 5 — Low Rhine (Niederrhein); 6 — Delta. A — Austria; B — Belgium; CH — Switzerland; D — Denmark; F — France; L — Luxembourg; NL — Netherlands, and B — Lake Constance (Bodensee). (From Kinzelbach 1982).

ity of water flow is between 0.9 and 1.5 m s^{-1} in some stretches.

To countercheck erosion and sedimentation, 11 dams have been built. All are designed for hydropower generation and are equipped with locks for navigation. To ensure a safe and easy use of the waterway, the main river flow has been by-passed through an artificial canal on the French territory (from km 173, immediately below Basel, downstream to approx. km 227, Breisach). In the former stream bed of the Rhine, now known as the "Rest-Rhine", there is a very limited discharge of 15 - 30 m^3 s^{-1}, far too little to maintain permanently the former character of the landscape and to support the flora and fauna.

Another four dams were constructed at regular intervals in the stretch below the by-pass canal. At 295 km downstream (Strasbourg), a ship-canal connects the Rhine and the Rhone rivers. Farther downstream below this branching, another 3 dams were built and one more is being considered. Upstream, these dams have slowed the cutting of the river bed. However, below the last dam the scour continues. To reduce scouring, large quantities of gravel have been excavated from surrounding gravel pits and dumped into the newly eroded stream bed. This technique seems to be ecologically less harmful and less expensive than the continuation of dam construction (Felkel 1981).

A stretch with a rather high slope (about 3‰) known as the "Middle Rhine" (Mittelrhein) (Fig. 1, No. 4) is located approximately midway between the 510 and 640 km mark. Two large tributaries that join the Rhine within this stretch, the Main River (confluence at 500 km) and the Mosel River (confluence at 590 km), contribute yearly mean water discharges of about 200 and 300 m^3 s^{-1}, respectively. Both tributaries are dammed and navigable. The main characteristic of the Middle Rhine is swiftly flowing water over a rocky bed. Until 1974, navigation in this stretch has been difficult, but, it has never been a natural barrier for fish movements.

The "Low Rhine" (Niederrhein) (Fig. 1, No. 5) is a slowly flowing meandering watercourse, continuously silted by upstream erosion. Passing through the most populated and industrialized part of Germany, "Ruhrgebiet", the river is loaded with a variety of wastes. There are, with one exception, no natural side-waters such as oxbows and backwaters which join the main river channel. Instead, sand excavation takes place along the stream banks and even if these artificial water bodies were linked with the main stream, they would not substitute for the former function of the natural side-waters.

FIG. 2. The "Upper Rhine" by artist Peter Birmann (ca. 1800). Reproduction of the oil painting located in the Art Gallery in Basel, Switzerland.

Even the delta area (Fig. 1, No. 6), originally the most diversified part of the stream, has been completely changed. In the Netherlands, all but one estuarine river mouth have been cut off from the surrounding environment by dams or sluices. About 80 to 85 % of the Rhine water reaches the North Sea near Rotterdam. Before branching into the delta the mean discharge of the Rhine is 2250 $m^3 s^{-1}$ with ranges from 13 000 to 620 $m^3 s^{-1}$. Wolff (1976) describes details of the degradation of the delta area, and stresses the negative impact of the Rhine watercourse on the adjacent brackish water areas of the North Sea. Attention has been paid also to macro-benthos and fishes (Peeters and Wolff 1973; Wijck 1971).

Hydrology

The stream-flow of the Rhine is well balanced. Hess (1959) puts the ratio between the lowest low water and the highest high water as 1:16 on the Upper Rhine and 1:20 on the Lower Rhine. This relationship results from the superimposition of various influences, for instance, the role of the Lake Constance in stabilizing flows that are generated from melted snow in the Alps.As well the precipitation in areas of larger tributaries (e.g. Main, Neckar, Mosel) usually does not correspond with freshets in the water supply from the high Alps.

Peak discharge during summer months is caused mainly by melting snow in the Alps during the months of June and July (Fig. 3). Runoff from uplands, mostly precipitation form late fall, winter and spring, (Fig. 3) and the already mentioned Alpine water supply, causes two peaks of stream flow on the Upper and Middle Rhine. This relative stability of the stream-flow is of vital concern for navigation.

From the biological point-of-view, fluctuations in water flows and levels provide opportunity for fish movement between mainstreams and adjacent side-waters. Today, these side-waters are extremely rare. They exist only within a narrow part of the formerly wide flood-plain, which is flanked by high water berms on both sides of the river.

Stream Alteration and the Pollution Load

The Rhine is an excellent example of the negative effect of human impact on river biota and surrounding area. Some 40 million people live along the Rhine or in its vicinity. About 20 % of the world's chemical production occurs in the Rhine catchment; as well, the largest agglomeration of heavy industry in Germany (possibly in Europe) is located on the Low Rhine, the so-called "Ruhrgebiet".

The first and most devastating change in the water flow and periodic floods occurred in the 19th century and caused structural changes in the river bottom. The braided wild stretch of the Upper Rhine was concentrated into one main channel so that most of the side-waters were isolated,

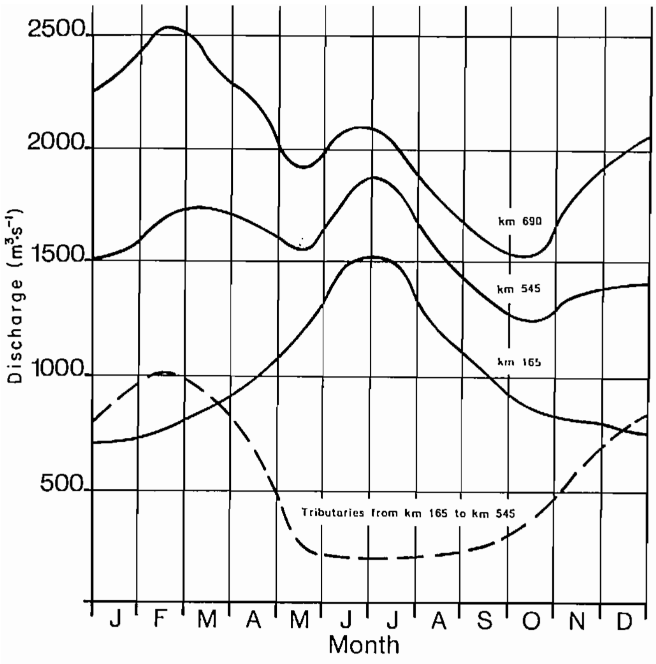

FIG. 3. Discharge of the Rhine according to long-term measurements at three stations: at km 690 (Low Rhine); km 545 (Upper Rhine); km 165 (below the High Rhine). Discharge of non-Alpine tributaries is indicated by a broken line (From Deutsches Gew. Jahrbuch, Rheingebiet 1974).

drained and converted to arable land. The meandering "Low Rhine" was straightened and the back-waters, with one exception, were separated from the main channel.

In the upper stretches of the Rhine provisions were made for safe navigation. Continuous improvements of safety measures allowed both day and night passage of radar-equipped ships causing wash and wave action from about 15 000 large vessels that pass up and down the river each year. The major part of the Upper Rhine was split into a by-pass ship canal and the former river bed, the "Rest-Rhine". Today, the discharge in the main river (> 10 % of the total discharge) cannot support original flora and fauna.

The construction of high water dams along both sides of the stream reduced flooding and prevented fish from moving laterally into formerly plentiful spawning areas. For the majority of species, spawning areas are alarmingly rare nowadays.

Municipal and industrial pollution has continuously increased since the beginning of this century causing the first damages to the aquatic fauna in general and the fishery in particular.

Half a century later, during the 60's, the pollution load reached its maximum. As a consequence, dramatic diurnal fluctuations in dissolved oxygen levels occurred, causing fish kills during periods of low water. Toxic substances, at both lethal and sub-lethal levels, wiped out several aquatic species. Heavy metals and chlorinated hydro-carbons made consumption of fish hazardous. By the mid-70's, water smelled of "phenol" and fish tasted badly.

Although the fauna and flora were studied and documented in detail at the beginning of this century by Lauterborn (1916, 1917, 1918), it is impossible to make quantitative comparisons between the past and the present situations. Knöpp (1957) undertook a most comprehensive survey of the general "pollution load". He studied all represented taxa throughout different stretches of the entire watercourse and compared them with taxa from the river before pollution began. The uppermost stretch, the High Rhine, has been the least affected in spite of many missing taxa present some 40 to 50 years ago (Lauterborn 1916, 1917, 1918). Knopp further attempted to quantify his observations. He made the least polluted stretch (below Lake Constance) equal to 1. All other stretches were contrasted with the first, i.e. the least changed stretch, thus measuring the impact of the "pollution load" downstream on the Rhine. His presentation, (Fig. 4) clearly documented the expected negative impact caused by human and industrial waste load (Fig. 4, No. 3). His method also revealed the self-purification ability of the stream, especially after water passes the Middle Rhine stretch (Fig. 4, No. 4) and the next heavy pollution load of the Low-Rhine (Fig. 4, No. 5).

In spite of mostly pessimistic prognoses, water quality has improved during the last 10 yr (Malle 1983). When all of the above chemical and biological results are taken together, a trend toward improvement seems to be undisputed, (Fig. 5, from Friedrich and Müller (1984) and LAWA (1985)). Comparable positive changes have been recorded for the Main River (Bernerth and Tobians 1979, 1984; Lelek and Tobias 1982; Lelek et al. 1984). The chemical and limnological properties of the Rhine water are dealt with in detail in several special publications of international committees, e.g. IAWR, IKSR, RIWA, LAWA, etc.

IAWR — International Working Group of the Waterworks in the Rhine Basin;

IKSR — Internationale Kommission zum Schutze des Rheins (Member States: Switzerland, France, Germany, Luxembourg, The Netherlands)

RIWA — Niederlandische Rijnkommissie Waterleidinigbedrijven (Dutch Rhine Commission of Waterworks)

LAWA — Landerarbeitsgemeinschaft Wasser (Working Group of Federal States of the Fed. Rep. of Germany)

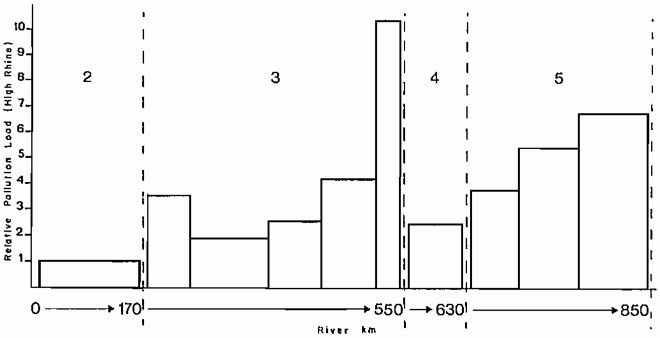

FIG. 4 "Pollution load" demonstrated by indicator organisms reveals the general downstream increase. The level of "load" has been standardized as 1 for the High Rhine (No. 2); No. 2 to 5 correspond with the stream stretches indicated in Fig. 1. (Slightly modified after Knöpp 1957).

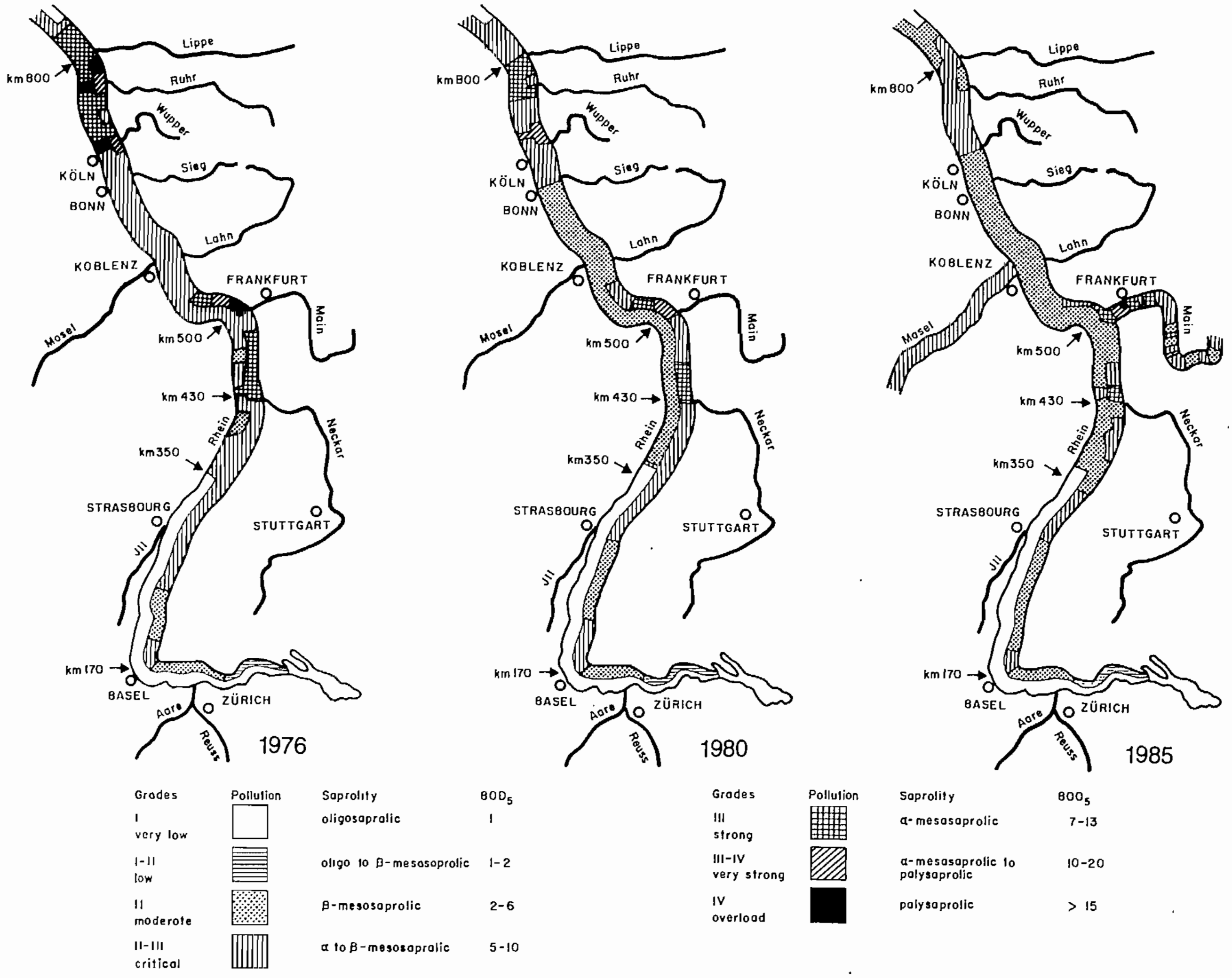

FIG. 5. Pollution from the High Rhine downstream to km 800 (German frontier) based on three combined parameters. Since 1976 to 1985 some improvement was recorded particularly on the Upper Rhine (Modified from Dtsch. Gew. Jhb. (1974) and LAWA (1985)).

Fish Fauna of the Rhine

The record of Rhine fishes dates back to a Latin publication by Ausonius (372 A.D.), in which he describes a Rhine tributary, the Mosel River. In his book *Mosella*, the author described 14 species from aesthetic and culinary points-of-view. The second oldest publication named *The Book about Bird, Fish and Animals* by Baldner (1666), apart from its historical value and its beautifully hand-coloured pictures, has an ichthyological value. The book gives precious information about large, attractive fish species but neglects small cyprinids. The first pioneering papers describing aquatic fauna were written by Lauterborn (1916, 1917, 1918) and Zschokke (1919, 1931); the latter deals with zoogeographical problems of the Rhine in general and fish distribution in particular.

Unfortunately, none can be exploited for quantitative comparisons. Taking into account several other authors, e.g. Sanders (1781); Nau (1787); Siebold (1863); Kirschbaum (1865); Leuthner (1877); Melsheimer (1878); Dosch (1899); and Böving (1981), we may conclude that 44 indigenous species formerly lived in the Rhine (Table 1). Including introduced species and some from Lake Constance which have been occasionally observed in the outflow from the lake, the list of species increases by another 16 taxa.

Introduced Species

Among purposely introduced fish species most effort has been directed toward the introduction of salmonids. Attempts to introduce *Hucho hucho*, and *Oncorhynchus tshawytscha* in 1880, have failed. Rainbow trout populations *Salmo gairdneri* introduced in 1881, depend on stocking and escape from fish culture; there is no verified record of natural reproduction of this species. Brook trout (*Salvelinus fontinalis*), introduced in 1879, are maintained by stocking but natural reproduction is unlikely.

The common carp, *Cyprinus carpio*, was probably introduced before written history (Balon 1974), and therefore it may be possible that the species has been living in the stream and adjacent waters for a very long time (Lelek 1983, 1987). Permanent stocking with the domesticated form, particularly with the mirror carp, continues in the catchment. Both feral and domesticated forms live in sympatry but maintain strict reproductive isolation (Lelek

TABLE 1. The occurrence of fish and lamprey species in the Rhine catchment area (excluding Lake Constance).
Legend: ● – common; ■ – rare; + – sporadical; ○ – not recorded; ? – improbable but not ruled out 2 – High Rhine; 3 – Upper Rhine; 4 – Middle Rhine; 5 – Low Rhine.

Families and species	Indigenous taxon	Exotic taxon	High, upper and middle Rhine (2 -3 -4)				Low Rhine (5)				Main				Mosel			
			until 1890	until 1950	1951-1975	since 1976	until 1890	until 1950	1951-1975	since 1976	until 1890	until 1950	1951-1975	since 1976	until 1890	until 1950	1951-1975	since 1976
Petromyzonidae																		
Lampetra fluviatilis LINNAEUS 1758	*		●	○	○	+	●	+	+	+	●	○	○	○	●	■	+	○
Lampetra planeri (BLOCH 1784)	*		●	●	+	○	○	○	○	○	●	■	■	■	●	■	+	■
Petromyzon marinus LINNAEUS 1758	*		●	○	○	+	●	■	+	+	●	○	○	○	●	○	○	+
Acipenseridae																		
Acipenser sturio LINNAEUS 1758	*		●	○	○	○	●	○	○	○	■	○	○	○	■	○	○	○
Clupeidae																		
Alosa alosa (LINNAEUS 1758)	*		●	○	○	+	●	○	○	○	●	○	○	○	●	○	○	○
Alosa fallax LACEPEDE 1800	*		○	○	○	○	●	○	○	○	?	○	○	○	●	○	○	○
Salmonidae																		
Hucho hucho (LINNAEUS 1758)		*	○	+	○	○	○	+	○	○	○	○	○	○	○	○	○	○
Oncorhynchus tshawytscha (WALBAUM 1792)		*	+	○	○	○	○	+	○	○	○	+	○	+	○	○	○	○
Salmo gairdneri (RICHARDSON 1836)		*	○	+	+	+	○	○	○	○	○	+	+	+	○	○	+	+
Salmo salar LINNAEUS 1758	*		●	+	○	+	●	+	○	+	●	○	○	○	●	+	+	○
Salmo trutta LINNAEUS 1758	*		●	+	○	+	●	○	+	+	●	○	○	○	●	+	+	+
Salmo trutta f. *fario* LINNAEUS 1758	*		●	+	+	+	■	+	+	○	●	○	○	+	●	■	+	+
Salvelinus alpinus (LINNAEUS 1758)	*		?	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Salvelinus fontinalis (MITCHILL 1815)		*	○	+	+	?	○	?	?	?	○	?	+	+	○	?	?	+
Coregonidae																		
Coregonus oxyrhynchus (LINNAEUS 1758)	*		○	○	○	○	■	○	○	○	○	○	○	○	○	○	○	○
Coregonus lavaretus (LINNAEUS 1758)	*		○	○	○	+	○	○	○	+	○	○	○	○	○	○	○	○
Thymallidae																		
Thymallus thymallus (LINNAEUS 1758)	*		■	+	+	+	■	○	○	○	●	+	■	■	●	■	+	+
Osmeridae																		
Osmerus eperlanus (LINNAEUS 1758)	*		○	○	○	○	●	+	○	+	○	○	○	○	○	○	○	○
Esocidae																		
Esox lucius LINNAEUS 1758	*		●	●	●	●	●	■	■	■	●	■	■	■	●	■	■	■
Cyprinidae																		
Abramis brama (LINNAEUS 1758)	*		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Alburnoides bipunctatus (BLOCH 1782)	*		●	■	+	+	■	○	○	○	●	○	○	○	●	+	+	○
Alburnus alburnus (LINNAEUS 1758)	*		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Aspius aspius (LINNAEUS 1758)		*	○	○	○	+	○	○	○	+	○	○	○	+	○	○	○	○
Barbus barbus (LINNAEUS 1758)	*		●	■	○	+	●	■	○	○	●	■	■	■	●	●	■	+
Blicca bjoerkna (LINNAEUS 1758)	*		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Carassius auratus (LINNAEUS 1758)		*	●	+	■	■	●	+	■	■	○	+	+	■	○	○	○	+
Carassius carassius (LINNAEUS 1758)	*		●	+	+	○	●	+	+	+	●	+	○	○	●	+	+	+
Chondrostoma nasus (LINNAEUS 1758)	*		●	■	+	+	●	○	○	○	●	+	+	+	●	■	■	■
Ctenopharyngodon idella (VALENCIENNES 1844)		*	○	○	○	+	○	○	○	○	○	○	○	+	○	○	○	○
Cyprinus carpio LINNAEUS 1758		*	●	■	■	+	●	■	■	+	●	■	■	■	●	■	■	■
Gobio gobio (LINNAEUS 1758)	*		●	■	+	■	●	■	+	■	●	■	■	■	●	■	■	■
Hypophthalmichthys molitrix (VALENCIENNES 1844)		*	○	○	○	+	○	○	○	○	○	○	○	○	○	○	○	○
Leucaspius delineatus (HECKEL 1843)	*		?	○	○	○	■	○	○	○	■	○	○	+	○	○	○	○
Leuciscus cephalus (LINNAEUS 1758)	*		●	●	■	●	●	■	■	■	●	●	■	●	●	●	●	●
Leuciscus idus (LINNAEUS 1758)	*		●	○	○	+	●	+	+	+	●	○	○	○	●	+	+	+
Leuciscus leuciscus (LINNAEUS 1758)	*		●	●	■	●	●	●	●	●	●	●	■	●	●	●	●	●
Leuciscus souffia agassizi (VALENCIENNES 1844)	*		○	+	○	○	○	○	○	○	■	○	○	○	○	○	○	○
Phoxinus phoxinus (LINNAEUS 1758)	*		●	○	○	○	■	○	○	○	■	○	○	○	?	○	○	○
Pseudorasbora parva (SCHLEGEL 1842)		*	○	○	○	○	○	○	○	+	○	○	○	?	○	○	○	○
Rodeus sericeus amarus (BLOCH 1782)	*		●	■	○	+	●	○	○	○	●	○	○	○	●	○	○	○
Rutilus rutilus (LINNAEUS 1758)	*		●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Scardinius erythrophthalmus																		

within the entire main stream, but often common in backwaters. The latter species was discovered in the Low Rhine but its present status is unknown. Of the cichlids *Astronotus ocellatus* has been recorded only once, from the heated effluents of the nuclear power plant on the upper Rhine. Its large size suggested it was released by an aquarist.

From the percids the pike-perch (Zander), *Stizostedion lucioperca*, is being increasingly introduced in the main stream and tributaries. Although it is uncertain whether or not this species was formerly in the Rhine (there was a historical connection with the Danube catchment at the end of the Tertiary via Lake Constance), this species has never established itself on an economically meaningful level. Initially, stocking began in 1882 and was intensified between 1928 and 1937. The overall increase in its abundance observed in recent years (1982–1985) was due to intensive stocking and successful reproduction. Yearlings were observed both in adjacent waters (mostly sand pits) and in the main stream as well. At some places the pike-perch is more common than the northern pike *Esox lucius* and has become the major top predator.

Changes of the Fish Community

Although it is not possible with any precision to record the past changes of the fauna and particularly the occurrence of economically less important species, trends in gross categories, i.e. abundant, rare and sporadic, can be demonstrated.

Records from old literature were used, as well as scattered notes from angling and naturalists' journals. The occurrence of fish species within the last two decades is based on catch records from a variety of Rhine localities; the newest information is provided by the author's electrofishing and netting samples.

The examination of old, partly unverifiable information revealed changes as follows: from 1890 to the end of 1985 three species of fish have not been observed (*Acipenser sturio*, *Cottus gobio*, *Platichtys flesus*). (See river sections 2 to 4, Fig. 1.) The most striking changes occurred between 1890 and 1950 when 27 species became less abundant. Similarly, from 1951 to 1975, 17 species of fish were regrouped to a lower category of occurrence. Within this period of post-war reconstruction and industrial boom, the destruction of the indigenous fauna seemed almost unavoidable. However, since 1976, a slight increase in the occurrence of certain species and the explosive recruitment of several other species have been recorded. Eighteen species were grouped into higher category of occurrence while only two species, *Carassius carassius*, together with the feral form of *Cyprinus carpio*, maintained the decreasing trend.

In the lowest Rhine stretch (Fig. 1, No. 5) corresponding to the metapotamon, 14 indigenous species were not recorded during the period of 1890 to the end of 1950, out of which at least 5 species ought to have been regular inhabitants; *Acipenser sturio*, *Alosa alosa*, *Alosa fallax*, *Coregonus oxyrhynchus*, *Cobitis taenia* and *Misgurnus fossilis*. According to the categories of occurrence, 33 species shifted into a category of lower occurrence by 1950. In the period 1951 to 1975, a drop in occurrence was recorded for 11 species. Since 1975, however, a slight recovery was observed — 11 species were placed in a category of higher occurrence and only 2 species *Salmo trutta* f. *fario* and *Cyprinus carpio* maintained the decreasing trend.

Records and comparisons of the past fish fauna with the existing one at the end of probably the worst ecological situation of the Rhine (1974–75) are summarized by (Lelek 1976a, b). The fish community at this time comprised only very few species. Roach, *Rutilus rutilus*, regularly dominated fish samples. Species composition underwent only small seasonal changes, (Fig. 6). In 1975, the positive influence on fish distribution and occurence of all deviations from the uniformity of the stream bed and the shore line was observed. The fish community was richer in number of species (Fig. 7) and in the quantity of individuals (Fig. 8), at all places where the monotony of the physical environment was disrupted.

Later sampling, particularly after 1976, shows a slow but continuous recovery of the fish community. Species with no special demands for quality of spawning substrate adapted to use both submerged plants, and gravel or rocks, ("phytolithophils" Balon (1975), eg. *Rutilus rutilus*, *Abramis brama*, *Alburnus alburnus*), and became more abundant; their numbers continue to increase.

The last sampling, done in October 1985, revealed a more or less similar composition of the fish community. In a stretch of the Upper Rhine (km 390 to 500) roach, *Rutilus rutilus*, dominated once again at 12 of 24 stations, followed by *Alburnus alburnus* and other more common cyprinids, with a locally higher abundance of perch *Perca fluvialitis* and eel *Anguilla anguilla* (Lelek unpublished date; Roth and Kinzelbach 1986). The occurrence of barbel, *Barbus barbus*, and *Chondrostoma nasus* increased: since 1983, several age-groups have been found (not just solitary individuals).

Eels play a special role within the fish community. Eel abundance, formerly dependent on the upstream migration of junveniles, (observed again in the Rhine in 1984–1985, Bless pers. comm.), is being maintained by intensive stocking throughout the entire catchment. Released eels move downstream and temporarily concentrate either along the rocky shoreline of the main river or invade the few remaining side waters of the Rhine. Additionally, these backwaters have been regularly stocked with elvers and juvenile eels. The examination of the occurrence of eels and their stomach contents revealed both high densities and intensive predation on young-of-the-year fishes (Lelek 1983; Lelek and Pelz 1986). The wild (or feral) form of the common carp was most affected by eel predation.

The assessment of eel density requires a special fishing technique (slow movement of the boat with the electric shocking device and prolonged application of the D.C. electric field on the spot). This technique avoids other fish species. When sampling is focused on eels at places with a highly diversified shoreline (mostly reinforced with boulders about 40 to 50 cms of size) eels were caught with great success while other species usually escaped. At these places the density of eels was 0.9 to 2.3 individuals ($\bar{x} = 1.2$) per metre of shoreline. If the "skill" of the fisher and the diversity of the shore is not considered, and only the catch itself is related to the fished stretch of the river, the yield ranges from 1.812 to 4.064 kg 100 m^{-1} ($\bar{x} = 3.384$) of the shoreline.

Lentic side waters, particularly those connected with the main stream, are very important for the development and maintenance of the fish community structure. These waters

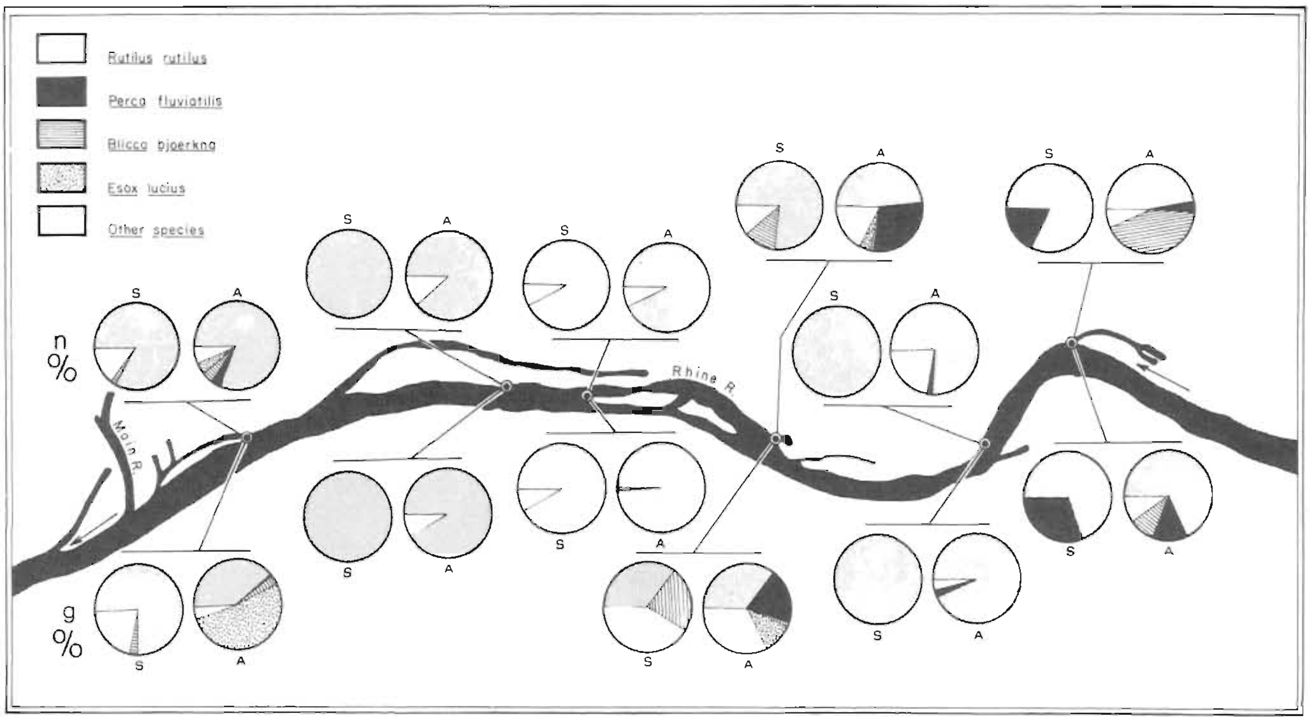

FIG. 6. The fish community at six stations of the Rhine at km 500 in percent of individuals (*n*) and percent of weight (*g*), recorded in spring (S) and autumn (A) months of the year 1975.

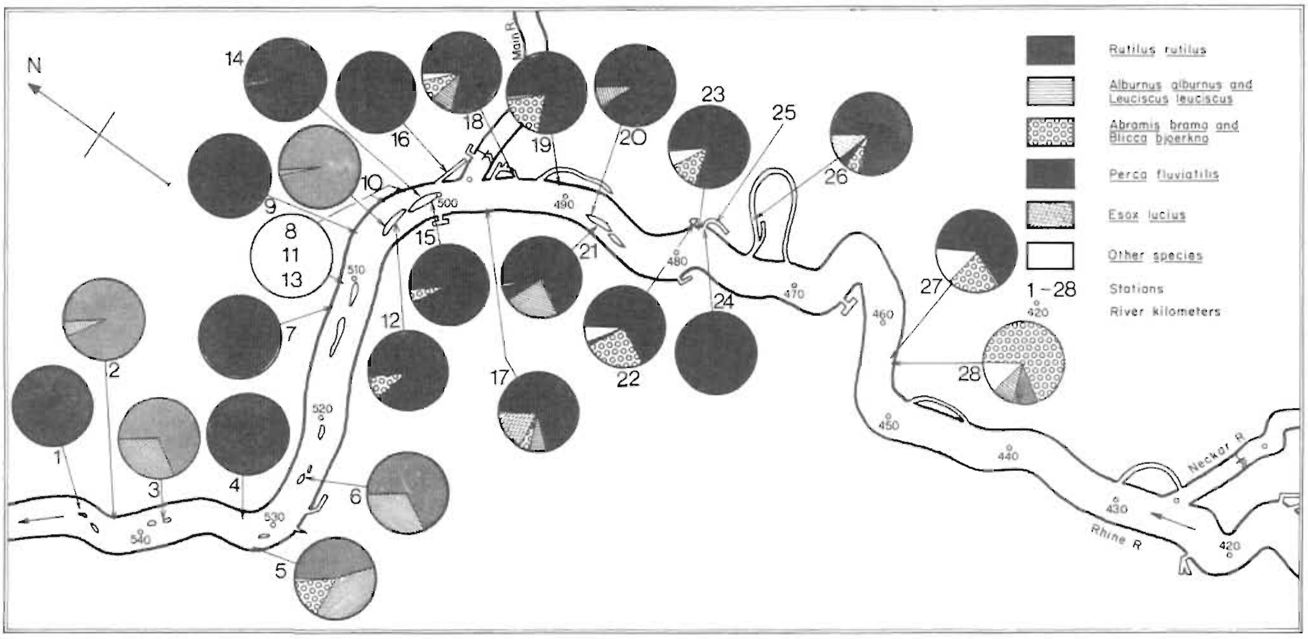

FIG. 7. The fish community in the Rhine, at 28 stations (km 550 to 450), in percent of the weight of respective species in 1976 (Lelek 1978).

provide spawning grounds for phytophilous species. During the years with the heaviest pollution load on the Rhine, (60's), these side waters served as refugia during spells of lethal or critical water-chemical changes.

Fish migrations between the mainstream and its side waters depends on permanent connections. Fish movements are guided by water levels, temperature, and seasons. In the spring, fish follow the warmer out-flowing water from the backwater and swim into the lentic environment (see Fig. 9 for roach). These patterns of movement were observed in two consecutive years by the author and by Meinert (1985). During late autumn and winter, when the whole area is often inundated, fishes are replaced by others from the main stream where they may remain in the backwaters until spring time to spawn.

The survival of fishes in these backwaters is not always

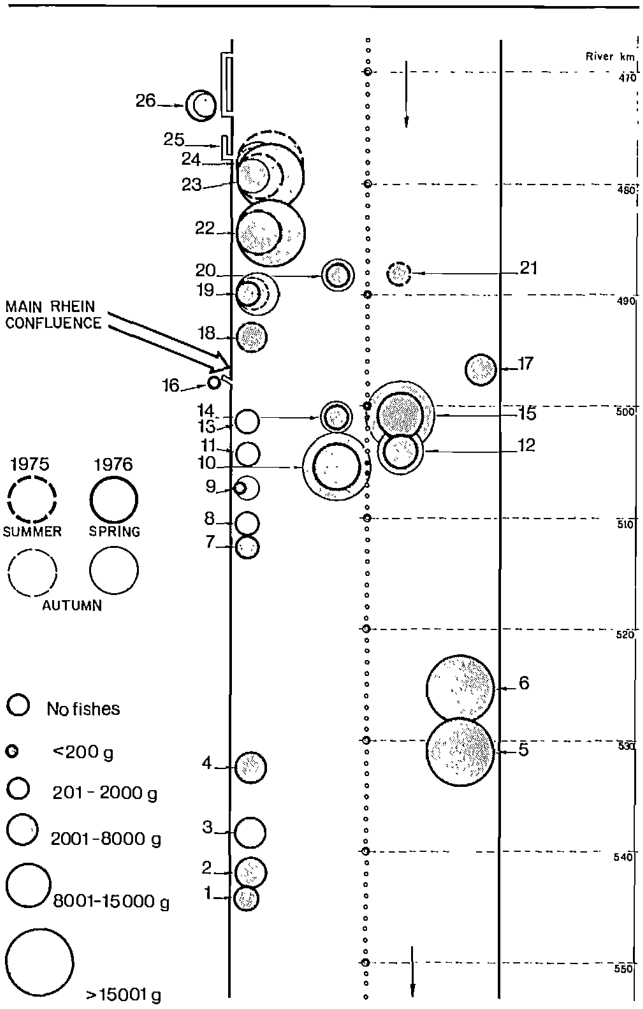

FIG. 8. Occurrence of fish in the Rhine River, at 26 stations, in different seasons of the year 1975 and 1976 expressed as total weight of all individuals. Weight was computed from 20 min. of electrofishing at all stations along the shore line and islands (Lelek 1978).

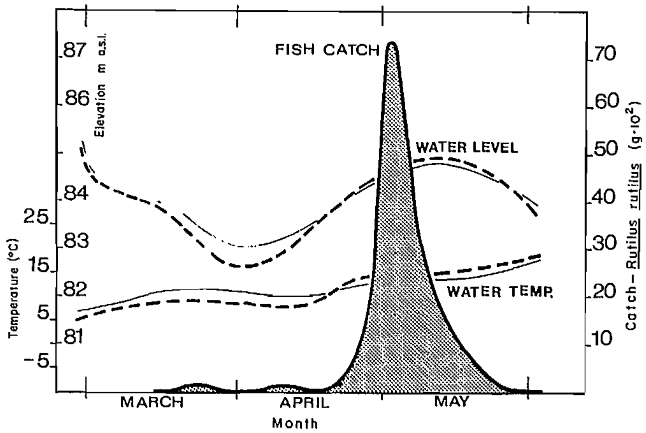

FIG. 9. Movements of fishes from the Rhine into the backwaters from March to the beginning of June. Left ordinate — water level and temperatures in the Rhine (solid line) and the backwaters (broken line); Right ordinate — catch of *Rutilus rutilus* in 1977. (Lelek 1981).

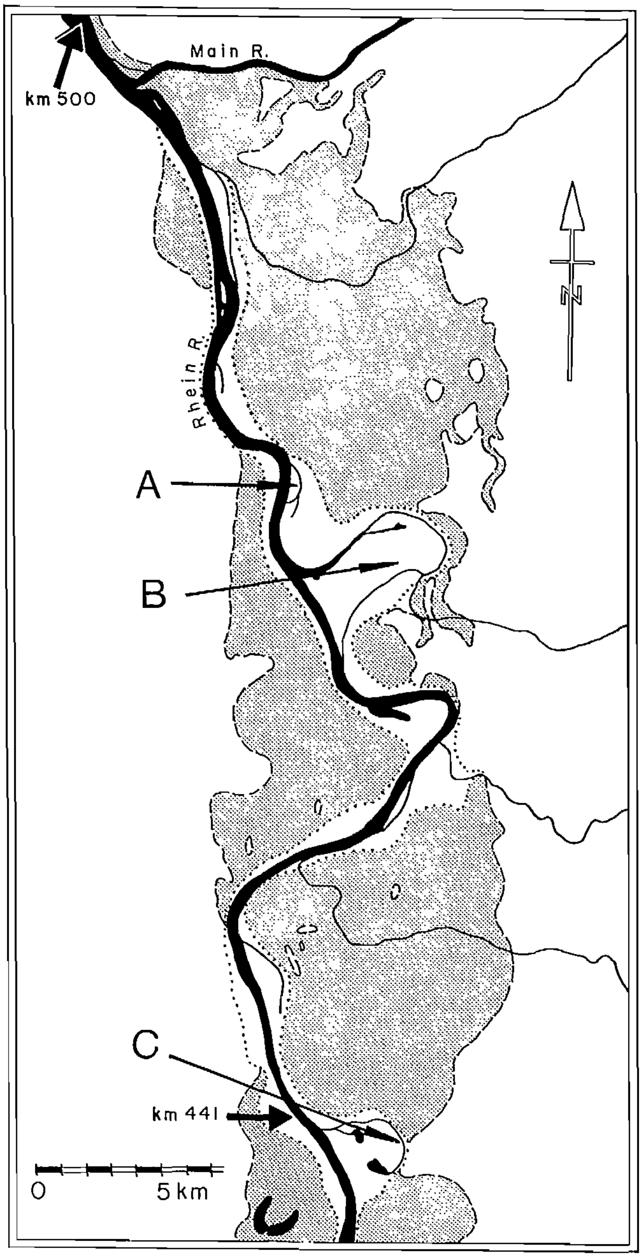

FIG. 10. The floods on the Upper Rhine (- - -), before Tulla's corrections, compared with the present maximal extent of high water marked with the dotted line. A, B, and C indicate the remaining side waters.

certain. Spawning and hatching were usually successful but many larvae became prey to the eels. As well, very often, juvenile cyprinids died from extremely high hydrogen ion concentrations. Survivors were found mostly in the vicinity of the confluence of the old arm with the main stream.

In backwaters, a correlation exists between sunshine, algal respiration, biogenic decalcification followed by high pH values and high mortalities of juveniles (Kieckhäfer 1978 and Schröder 1979). Junveniles of *Cyprinus carpio* are the most sensitive to this relationship and percids the least. This partially functioning side water is in the Rhine stretch between km 441 to 500 (Fig. 10).

The Rhine Fisheries

An analysis of the fishery of the Rhine would seem to be a task for a historian rather than for a fishery biologist. The decline of the artisanal fishery began shortly after the straightening of the stream, c. 1850, and continued as the stream developed into a ship canal (from 1850 to 1920). Since 1915, however, a continuous and irreversible decline of catches has occurred. The older literature has provided information about the yield from different Rhine stretches, mostly from the High and Upper Rhine and from Dutch territory. Catch records described landings of the valuable species, salmon, strugeon, sea trout and Allis shad, *Alosa alosa* almost exclusively. As far as other species are concerned, only exceptionally high or unusual catches were ever mentioned.

It was not easy to make a summary of fish catches from the whole Rhine because of difficulties in international cooperation. Even within one country, the Federal Republic of Germany, it was complicated to develop an overview of fish catches. Each federal state has slightly different fishery legislation and does not have an equally consistent approach to fishery management.

Catches of strugeon, *Acipenser sturio*, and of salmon, *Salmo salar*, document the regressive trend most convincingly. Apart from the general regression, in both cases an abrupt decline of catches is evident which to some extent corresponds with negative environmental changes (Fig. 11 and 12). In the case of the sturgeon, undoubtedly fishing intensity played its part, and, intensified by man-induced changes of the stream, removed this species from the fauna and the fisheries (Vaas 1968; Verhey 1949). Salmon catches, definitely more important economically throughout the entire water course, demonstrate convincingly several steps of environmental deterioration and a short-lived "improvement". The fluctuation of catches reflects the partial destruction of spawning grounds, frantic efforts in artificial propagation, negative changes linked with the intent to make the stream fully navigable and even the relative improvement of water quality which occurred shortly after the 2nd World War as a consequence of the destruction of industry in Central Europe. Surveys presenting the decline of fishery are based on catch records, e.g. Trahms (1955) or on the decreasing number of artisanal fishermen (Büger 1926 and Koch 1955). The number of full-time fishermen on the Upper Rhine dropped from 400 to 60 between 1850 to 1900 on the river at the 120 km mark.

All efforts to compensate the fishermen were either abortive or insufficient. The majority took up a different occupation or continued as part-time fishermen only. Official government support went only to the artificial propagation of salmon, rediscovered in Vosges (Vogesen) on the French side of the Rhine in the year 1853, and copied dynamically on the German side since 1859. (The discovery of the artificial propagation of trout by Jakobi 1709, 1784 was forgotten!!; for details see Meyer-Waarden 1972). Propagation in Luxembourg on the Mosella River, and particularly in Holland was carried out simultaneously. The mutual effort to improve the salmon stock and fishery resulted in the "International Treaty of Salmon Fishery — 1855" between of The Netherlands, Germany, and Switzerland. The "Treaty" dealt with topics like open and closed seasons, the use of special gear, and stocking with the hatchery reared juveniles. The "Treaty" also tried to guarantee (or at least to support) the protection of natural spawning grounds in the Rhine and its tributaries. It strongly recommended the use of hatcheries for restocking salmon. Results were surprisingly good; the Upper Rhine regularly received 4 to 6 million yolk-sac salmon a year. These efforts probably maintained catches during the period of 1890 to 1910–15; but, in spite of all these measures, stocks continued to decline. Ehrenbaum (1895) was convinced that artificial propagation could not rescue the Rhine salmon stock and thus translated and re-evaluated the earlier Dutch version of Hoek's paper, which also advocated the protection of natural spawning grounds.

Trahms (1955) summarized very pragmatic reasons that lead to the reduction and near destruction of the Rhine fishery. He postulated that (1) the Rhine was a 'virgin' stream roughly until 1765; (2) the first irreparable setbacks were due to 'rectification' of the stream followed by the development of steamship traffic; (3) the next worsening of environmental quality was due to the expansion of industry (c. 1850) linked with the urbanization of the area surrounding the Rhine. The impact of industrial urbanization resulted in an increase of pollution and continued, without interruptions or improvements, until shortly after the 2nd World War. Denzer (1966) described another setback using catch statistics. Fish catches were reduced between 1949 and 1953 on the Low Rhine as follows: the catch of salmon from 3306 kg to 30 kg (-99 %), the catch of eel from 11 875 kg to 1732 kg (-85 %) and the catch of the remaining species from 33 894 kg to 3574 kg (-89 %).

Salmon fishing has been described by many authors (e.g. Steinmann 1925). The references to the "good old times" have a flavour of nostalgia; nowadays, it is difficult to believe that they ever existed. The disappearance of shad *Alosa alosa* almost coincided with the disappearance of salmon. The last sturgeon was caught on the Low Rhine in 1941. After salmon lost its importance in the fishery and virtually disappeared, the eel was the next species to support the fishery. The reason to turn to the eel was their relative abundance. While this species was easily marketable, established fishing methods were not suitable.

Upstream from Holland the use of a fishing gear called "Aalshocker" became customary. This passive gear is basically a long net-bag hanging on a beam which is attached to the side of a boat. Both the boat and the net are anchored in the swift water current, usually over the deepest place. The net is set in such a way as to be opened by the incoming water current in the top layers of the water column, thus filtering the downstream migrating (or drifting) eels. This net yielded the best results at night during the dark phase of the moon. The gear was selective enough to catch the preferred large eels in their "silver" development stage. Catches were sufficient to enable the remaining fishermen to survive. However, growing industrial activity and the communities surrounding the river eventually polluted the Rhine and some of its tributaries to such an extent that the ascent of eels from the estuaries almost ceased. As a quick remedy, eels were stocked throughout the catchment. Their supplies came from many areas including estuaries of large European rivers which empty into the Atlantic (or North Sea), mostly from France.

In spite of all attempts to make use of the eel as the only species able to survive heavily polluted waters, a second set-

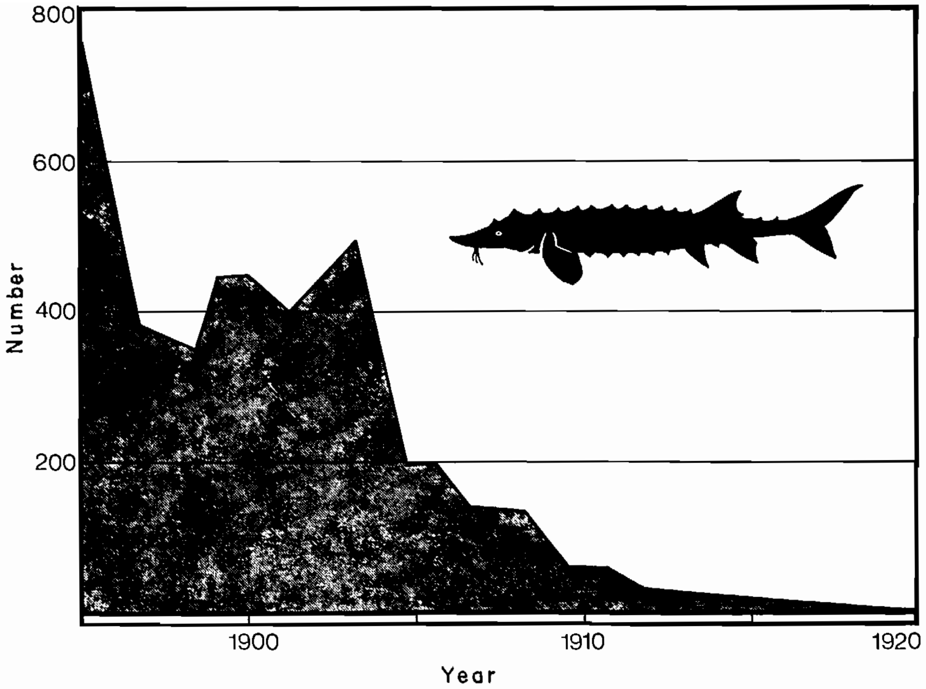

FIG. 11. Catches of the sturgeon, *Acipenser sturio*, in the Low Rhine. (From Trahms 1955).

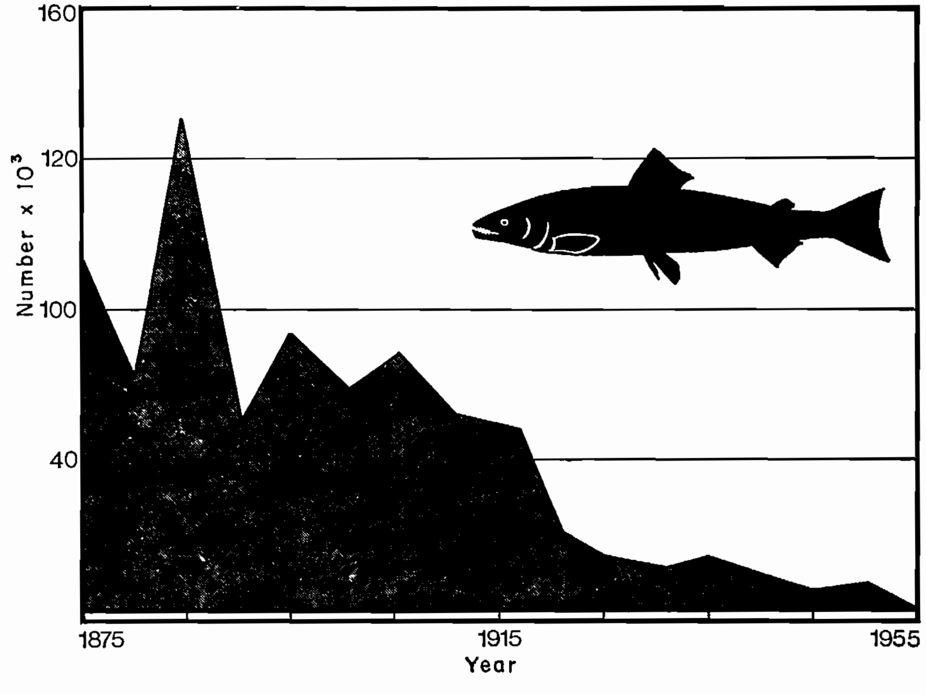

FIG. 12. Catches of the salmon, *Salmo salar*, in the Rhine. (From Trahms 1955).

back to the fishery was unavoidable. For instance one fisherman in the Middle Rhine caught 650 kg eels yr^{-1}, in 1946. In 1964, the catch had diminished to 2.3 % of the former amount. The overall catch, including the less marketable species, was 92.5 % lower within the same periode (Bless 1979, 1981). Similar but less dramatic reduction of catches was reproted by Kuhn (1976) from the Upper Rhine. Kuhn also refers to obstacles to fishing eels, particularly the clogging of nets with *Sphaerophilum natans* during the peak period of organic pollution, which finally contributed to the demise of this fishing technique. The period of the heaviest pollution coincided with an increased intensity of waterway traffic on the Rhine, particularly when night traffic with radar-equipped ships began. The shipping had economical priority over the fisheries so that the 'Aalshocker' could not be positioned at places to catch seaward moving eels, i.e.

over deep water close to banks. According to an estimate by Kuhn (1976), in 1932 about 200 units operated on the German stretch of the Rhine, and altogether about 300 to 400 'Aalshockers' in the system. At the peak of the worst time, this type of fishery was almost impossible because of above mentioned reasons. It has not recovered even today.

At present, it is highly probable that the majority of eels descent without any great fishing pressure. A small portion are caught by the sport fisher and another, not exactly identifiable proportion of the downstream migrating stock is fished by artisanal fishemen. Today, traps are set only at a few sites on the stream, and intensive fishing in backwaters is limited to short seasons of the year to prevent disturbances of breeding and migrating birds. Electrofishing is effective only close to the shoreline (within 2–3 m) but has not been legalized in all federal states, notwithstanding it is the only effective method of eel fishing that remains.

When the disastrous situation of the freshwater fishery was finally appreciated, some effort was put toward maintaining the last remaining resource of eels through stocking. (Meyer-Waarden 1965–67). This activity was successufl in supporting a fishery but did little toward the rehabilitation of the fish community. Eels were released almost everywhere along the river system but before they reached the stage of downstream migration their predatory behaviour and their high abundance threatened many fish communities in the rhithral (see Balon et al. 1987; Anon. 1986; Lelek and Pelz 1986).

Fish Yields

Fish yield data come from a variety of official statistics and reports (Anon. 1976). Procedures of data recording ie. with the catches of the individual sport fisher, as well as the professional fishermen, have not been carefully standardized, hence all provided information has been interpreted with caution. Yield data come mostly form stretches or areas where the fishing effort promised better catches and the desired species. Yield information does not reflect the actual productivity of the stream. The information is biased because it reflects data from relatively good fishing grounds for more valuable species (pike-perch, eel, common carp, pike), yielding fish because of focused efforts. Fishing grounds where only less valuable species are expected (eg. roach, bream, bleak, etc.) have been traditionally underfished as there is little market demand for the latter species; they are also less attractive for sport fishing.

The recorded yield in the High Rhine (Fig. 1, No. 2) was estimated at 37.6 kg ha^{-1} yr^{-1}. The values from lentic impoundments range between 21.1 kg ha^{-1} and 61.8 kg ha^{-1}. The highest yield of 67.7 kg ha^{-1} came from one flowing stretch between the impoundments. One early yield estimate (c. 1800) for the Upper Rhine (Fig. 1, No. 3) was calculated by Kriegsmann (1970) to have been as high as 240 kg ha^{-1}. This high estimate likely included the migratory species salmon and seatrout as well as shad. Shortly after making the stream navigable, yields dropped to only 45 kg ha^{-1}. The regularly flooded backwaters provided a yield of 115 kg ha^{-1}; in the impounded stretches of the Upper Rhine the yield was 42.4 kg ha^{-1}. In the backwaters, separated from the Rhine, the yield varied between 63 and 84 kg ha^{-1}. The yield of the Low Rhine was estimated to be 45 kg ha^{-1} (all data from Kriegsmann 1970). A yield as high as 200 kg ha^{-1} was recorded by Kuhn (1976) from the backwaters connected with the Rhine at approximately 350–380 km downstream. Our observations from the Rhine side waters (km 470–480) revealed extremely high, seasonally dependent fluctuations of the total ichthyomass ranging between 3.9 kg ha^{-1} and 1187 kg ha^{-1} (Lelek 1978). According to the catches of the last professional fishermen in this locality, the yield, very roughly estimated, was between 125 to 270 kg ha^{-1} between 1980 and 1984. The above mentioned yield does not include the catches of sport fishermen, which may add another 10–15 % to the above mentioned weight of the yield.

Fish Stocking

Fish stocking is concentrated on the side waters with very little on the main stream. Several species are regularly released: the eel (in the stage of "glass-eel"), the pike and pike-perch as young-of-the-year, the common carp mostly the domesticated form, the mirror carp and the tench, *Tinca tinca*, as 2-yr olds. Trout (brown and rainbow) are released as fingerlings. From the cyprinids, the roach *Rutilus rutilus* is occasionally released in larger sizes (ready to catch). Stocking costs are covered partly by fishing organizations and heavily subsidized by the government. It is unlikely that fish stocking contributes much toward the improvement of the needed balance between predatory and forage fishes. The stock of predatory fish, which has almost no chance of spawning in the Rhine has to be maintained artificially. Moreover, fishing pressure from the combined efforts of all types of fishermen prevents the development of stable predatory populations which would control the overabundance of the dominating cyprinids. Eels are not stocked into large rivers but elsewhere with already mentioned negative consequences when released into the existing backwaters. The present massive releases of glass eels (1987) after the last accident in Basel (Bale) in November, 1986, may be detrimental for the rehabilitation of the fish fauna in general, particularly in the Upper Rhine.

The Tributaries to the Rhine River: The Main and the Mosel Rivers

The Main River (Fig. 1) deserves to be mentioned as this stream is the most important tributary to the Rhine. In the past, it was one of the most productive rivers; it was made partly navigable in 1850, and it contributed most to the Rhine pollution in the last 20–30 years.

The history of the fish fauna is well known, see e.g. Leiblein (1853), Stadler (1961), and has been described several times by Klausewitz (1972, 1973). The limnology of the Main River has been studied in detail, (see Bernerth and Tobias 1979). The gradual repopulation of this stream, which totally deteriorated in the 70's, is described by Lelek and Tobias (1982) and Lelek et al. (1984). The succession of changes is presented in Fig. 13 and 14; for the simple fish community based on dominant species see Fig. 15.

The Mosel River, the left Rhine tributary (Fig. 1) was mentioned in ancient times by Ausonius (372 A.D.), and very little has been reported since. A more recent communication, Rosengarten (1954), Jens (1966), and the new one, Pelz (1985) made a contribution to the fish fauna and to the function of fish ladders. Their communications reveal great

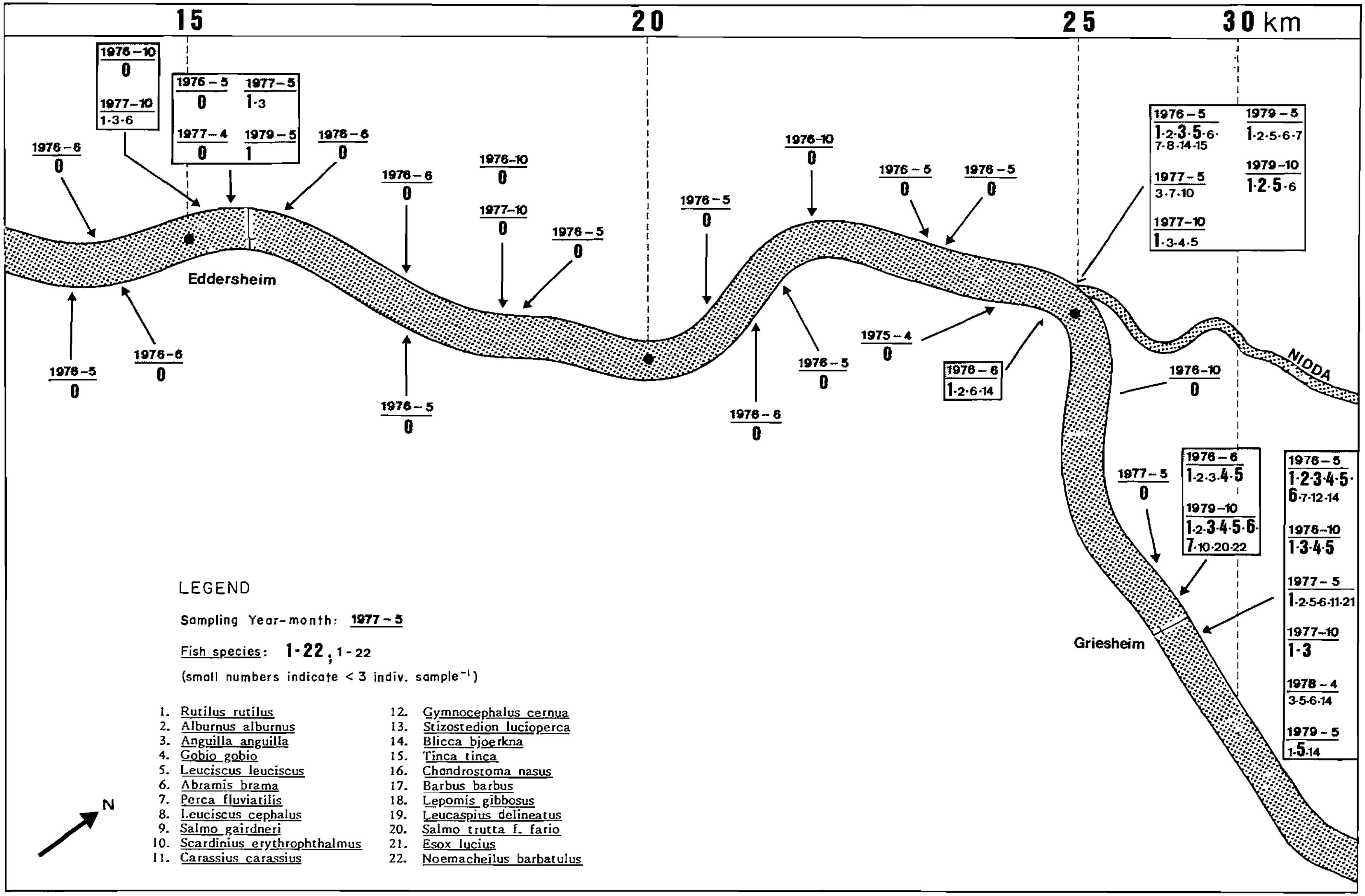

FIG. 13. The occurrence of fish species in the Main River at the end of the most critical pollution period (1975-79) (Lelek et al. 1984).

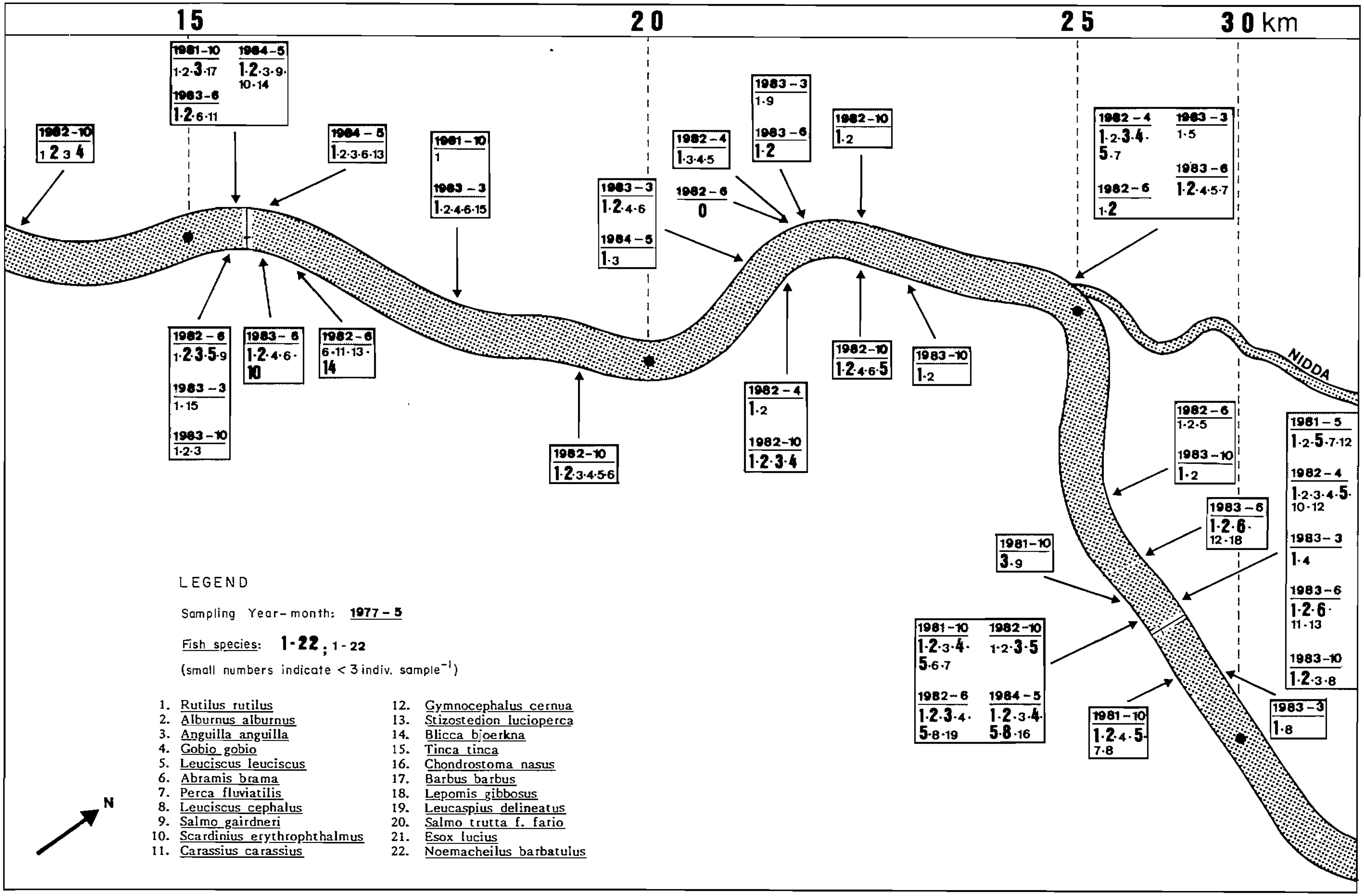

FIG. 14. The occurrence of fish species in the Main River during the period of stream recovery (1981–84) (Lelek et al. 1984).

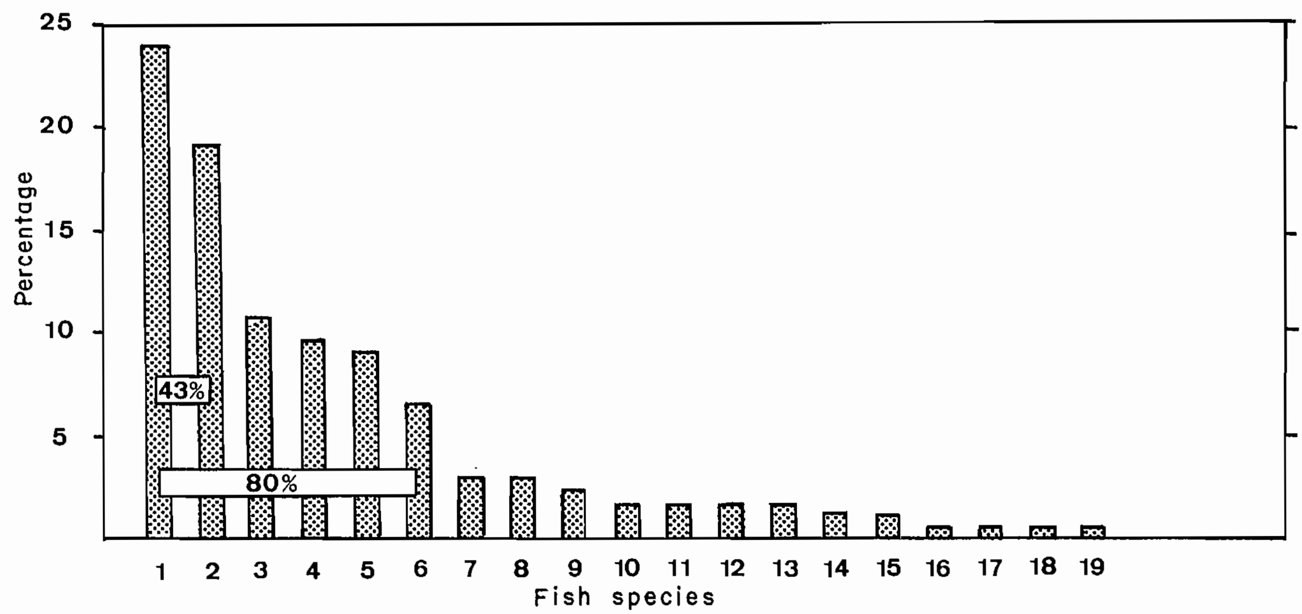

FIG. 15. The fish community in the Main River between 1981 and 1984. For species see the legend in Fig. 13 or 14 (Lelek et al. 1984).

similarities in the fish community from a canalized tributary (Fig. 16) to the main stream, the Rhine (Fig. 15). The fishery in the Mosel, though not stressed by pollution as severely as the Rhine, requires the same ecotechnical approach to restore the environment as does the Rhine and Main in order to make it less dependent on fish stocking. Again, the main task is to increase permanently the stock of predators.

Mitigative Measures

1) The present effort to improve the quality of the water has to be maintained and/or accelerated. The main polluters (i.e. the chemical industry) have already built purification plants. The public, together with the government, have to continue to demand further improvements. The results of these investments to date are clearly detectable both on the Rhine itself and on the major tributaries. A large scope of possible future improvements is advisable, e.g. the construction or remodelling of inefficient water purification plants. Further improvements can be achieved by a modification of certain forms of agriculture: a reduction of artificial fertilizers applied on soils that leach easily would help considerably to reduce the eutrophication of waters.

2) The functioning side waters of the Rhine have to be kept permanently connected with the main stream.

3) All side waters, both the natural ones which were cut-off and the artificial waterbodies (mostly left after sand excavation) have to be artificially connected with the main stream (Schäfer 1978).

4) All conservation measures have to be guided with the aim to reestablish the functioning hydrological system of the floodplain within its existing range. (see Bayley 1988).

5) All attempts to create protective zones or sanctuaries have to be coordinated, with contributions by limnologists, botanists and zoologists, bearing in mind 4, above.

6) The use of the floodplains for recreation, both land and water, has to be restricted to special places, especially for sportfishing, boating and bird watching.

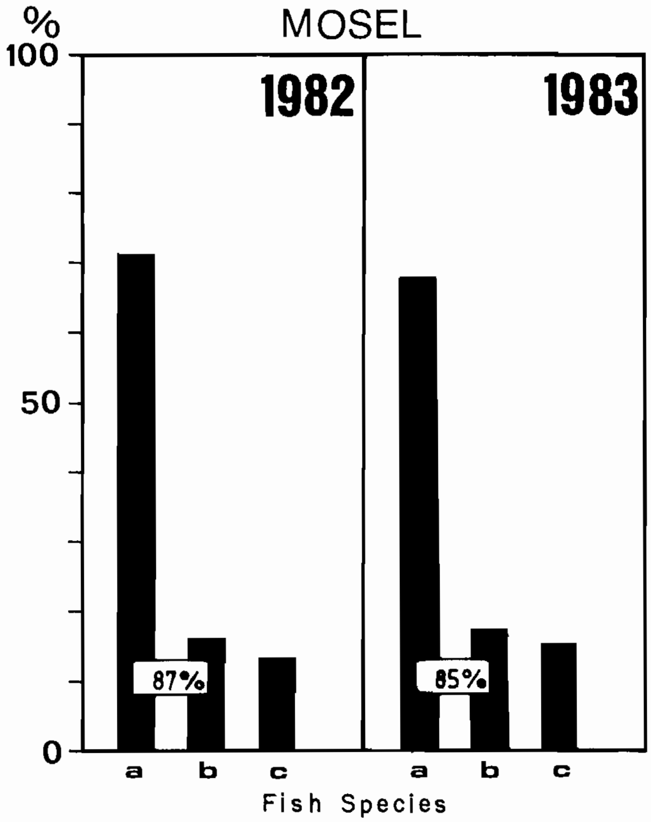

FIG. 16. Dominance in the fish community of the Mosel River; a= roach *Rutilus rutilus*; b= bleak *Alburnus alburnus* and c= eight remaining species (From Pelz 1985).

7) Practical fishery management has to be guided by the most recent knowledge of ecology and fish biology.

8) Rapid improvements might be achieved by the introduction and immediate implementation of artificial spawning substrates for predatory species at all suitable localities within the whole watercourse.

9) The establishment of an international, centrally organized fishery advisory unit for the whole watercourse has to be considered.
10) Scientific studies of the man-made ecosystem of the existing Rhine have to be encouraged in order to gain more theoretical and basic information about interactions.

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References

ANON. 1976. Umweltprobleme des Rheins. Der Rat von Sachverständigen für Umweltfragen. 3. Sondergutachten. Kohlhammer, Stuttgart and Mainz. 258 p.

1986. Das Vorkommen der Fische in Fliessgewässern des Landes Hessen. Hessisches Ministerium für Landwirtschaft und Forsten. (Based on the work of M. Barlas, A. Lelek, W. Meinel, G.R. Pelz and H.G. Pieper, 72 p.)

AUSONIUS, D.M. 372 A.D. Mosella, (Latin text) translated by W. John, 1980, into German. Trier. 150 p.

BALDNER, L. 1666. Das Vogel-Fisch und Thierbuch des Strassburger Fischers. *In* R. Lauterborn [ed.] introduction.

BALON, E.K. 1974. Domestication of the Carp, *Cyprinus carpio*. Roy. Ont. Mus. Life Sci. Misc. Pub. 37 p.

1975. Reproductive guilds of fishes: a proposal and definition. J. Fish. Res. Board Can. 32(6): 821-864

BALON, E.K., S.S. CRAWFORD, AND A. LELEK. 1987. Fish communities of the upper Danube River (Germany, Austria) prior to the new Rhein-Main-Donau connection. Environ Biol. Fish. 15(4): 243-271.

BAYLEY, P.B. 1989. Aquatic environments in the Amazon Basin, with an analysis of carbon sources, fish production, and yield, p. 399-408. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

BERNERTH, H., AND W. TOBIAS. 1979. Der Untermain — ein flussökologisches Portrait. Kleine Senckenbergreihe, Kramer, Frankfurt. 10: 1-64.

1984. Zur Kenntnis der Trophie- und Sauerstroffbedingungen im unteren Main. Cour. Forsch. -Inst. Senckenberg, 70: 5-33.

BLESS, R. 1979. Die Fisch- und Weichtierfauna des Rheins bei Bonn. Rheinische Landschaften, 16: 10-11.

1981. Beobachtungen zur Muschelfauna des Rheins zwischen Köln und Koblenz. Decheniana (Bonn) 134: 234-243.

BÖVING, H.P. 1981. Die Fischfauna des Rheinstromes und seiner direkt angrenzenden Altwässer im Niederrheingebiet. Decheniana, Bonn. 134: 260-273.

BÜRGER, F. 1926. Die Fischereiverhältnisse im Rhein im Bereich der preussischen Rheinprovinz. Zeitschrift f. Fischerei u. deren Hilfswiss. 24: 217-399.

DENZER, H.W. 1966. Beiträge über die Schädigung der Berufsfischerei am Rhein im Lande Nordrhein-Westfalen. Fischwirt 16(10): 253-264.

DEUTSCHES GEWÄSSERKUNDLICHES JAHRBUCH, RHEINGEBIET 1974. Landesamt für Gewässerkunde, Mainz.

DOSCH, L. 1899. Die Fischwasser und die Fische des Grossherzogtums Hessen mit Einschluss der Fischerei und Gesetzeskunde. Giessen. 152 p.

EHRENBAUM, E. 1895. Statistische und biologische Untersuchungen an in den Niederlanden gefangenen Lachsen. Mitt. der deutschen Seefischerei- Vereinigung(1895): 57 p. (Based on the report of P.P.C. Hoek, published in Verslag Staat Nederlandsche Zeevisscheryen, 1893).

ELSTER, H.J. 1974. Das ökosystem Bodensee in Vergangenheit, Gegenwart und Zukunft. Schr. VG Bodensee, Friedrichshafen 92: 233-250.

ELSTER, H.J., AND W. EINSELE. 1938. Beiträge zur Kenntnis der Hydrographie des Untersees (Bodensee). Int. Rev. Gesamten Hydrobiol. 36: 241-284.

FELKEL, K. 1981. Das Problem der Sohlenstabilisierung des Oberrheins und die Naturversuche mit Geschiebezugabe. Beiträge zur Rheinkunde, Koblenz. 33: 20-35.

FRIEDRICH, G., AND D. MÜLLER. 1984. Rhine, 265-315. *In* B.A. Whitton [ed.] Ecology of European Rivers. Blackwell, London. 644 p.

HARTMANN, J., AND W. NÜMANN. 1977. Percids of the Lake Constance, a lake undergoing eutrophication. J. Fish. Res. Board Can. 34(10): 1670-1677.

HESS, F. 1959. Probleme des Hochwasserschutzes am Niederrhein. Gewässer und Abwässer 23: 1-44.

JENS, G. 1966. Die Moselfischerei vor und nach dem Ausbau des Stromes. Landschaft und Moselbau. 44 p.

KIECKHÄFER, H. 1978. Aalfangerträge von Altrheinen und Baggerseen. Arbeiten des Deutschen Fischerei- Verbandes 26: 75-82.

KINZELBACH, R. 1982. Veränderungen der Fauna im Oberrhein, p. 66-86. *In* N. Hailer [ed.] Natur und Landschaft am Oberrhein, Versuch einer Bilanz. Verlag d. Pfälzischen Ges. zur Förderung der Wiss.: Speyer.

KIRSCHBAUM, C.L. 1865. Die Reptilien und Fische des Herzogthums Nassau. Verzeichnis und Bestimmungstabelle. Nass. naturwiss. Jahrbücher, 17-18. 46 p.

KLAUSEWITZ, W. 1972. Zustandsbilder des Untermains I. Der natürliche und der kanalisierte Fluss; Zustandsbilder des Untermains II. Die frühere Abwasserbelastung des Flusses. Natur und Museum, 102(3): 81-92; 102(6): 214-220.

1973. Über die abwasserbedingten Schwankungen des Fischbestandes im Untermain in den Jahren 1970-1972. Der Fischwirt 23(6): 111-114; (7): 115-116.

KNÖPP, H. 1957. Die heutige biologische Gliederung des Rheinstroms. Deutsche Gewässerkundliche Mitteilungen, 1(3): 56-63.

KOCH, W. 1955. Die Rheinfischerei in Vergangenheit, Gegenwart und Zukunft unter dem Einfluss der Rheinkorrektion und Energiewirtschaft. Arch. f. Hydrobiol. 22(3-4): 369-380.

1973. Zur Geschichte der Mainzer Fischerzunft. Mz. Naturw. Arch. 12: 5-21.

KRIEGSMANN, F. 1970. Gutachten über die Rheinfischerei und die Wirkung der Teilkanalisierug zwischen Breisach und Kehl. In: Anon. 1976.

KUHN, G. 1976. Die Fischerei am Oberrhein. Hohenheimer Arbeitzen. Ulmer, Stuttgart. 83: 196 p.

KUNZE, E. 1982. Flussbauliche Massnahmen am Oberrhein von Tulla bis heute mit ihren Auswirkungen — 150 Jahre Eingriff in ein Naturstromregime, p. 34-50. *In* N. Hailer [ed.] Natur und Landschaft am Oberrhein, Versuch einer Bilanz. Verlag d. Pfälzischen Ges. zur Förderung der Wiss. Speyer.

LAUTERBORN, R. 1916, 1917, 1918. Die geographische und biologische Gliederung des Rheinstroms I to III. Sber. Heidelb. Akab. Wiss., Math.-naturwiss. K1.B, 1916(6): 1-61; B, 1917(5): 1-70; B, 1918(1): 1-87; Heidelberg.

LAWA 1985. Die Gewässergütekarte der Bundesrepublik Deutschland von 1985. Published by LAWA (Ländergemeinschaft

Wasser) under chaimanship of Bavarian Interior Minister, München. 19 p.

Leiblein, V. 1853. Versuch einer Aufzählung der Fische des Maingebietes. Correspbl. Zool. Mineral. Ver. Regensburg, 7: 97–127; 183–185.

Lelek, A. 1976a. Changes of the fish fauna in some Central European Streams (Donau, Elbe, Rhein). Schriftenreihe Vegetationskunde 10: 295–308.

1976b. Ichthyology of the Upper Rhine River. Rev. Trav. Inst. Pêche marit. 40(3–4): 652–653.

1978. Die Fischbesiedlung des nördlichen Oberrheins und des südlichen Mittelrheins. Natur und Museum 108(1): 1–9.

1981. Population dynamics of fishes in the changing streams, p. 191–209. *In* H. Hoestlandt [ed.] Dynamique de Populations et qualité de l'eau: Formation permanente en écologie et biologie, Gauthier-Villars, Paris.

1983. Ichthyologische und fischereibiologische Arbeiten in den hessischen Altrheinen. Naturschutz und Landschaftspflege in Hessen, Jhb. 1981/82: 54–57.

1987. Notes on the reproductive ecology of the feral form of the common carp *Cyprinus carpio carpio*, in the Rhine River. Proc. V Congr. europ. Ichthyol., Stockholm 1985, p. 169–173.

Lelek, A., and G.R. PELZ 1986. Untersuchungen zur ökologischen Bedeutung von Aalen Anguilla anguilla und Aalbesatzmassnahmen. Cour. Forsch.-Inst. Senckenberg 85: 57–64.

Lelek, A., R. Pelz, and T. Polpakdee. 1984. Sukzessive Wiederbesiedlung des Mains unterhalb der Stadt Frankfurt mit Fischen. Cour. Forsh. Inst. Senckenberg 70: 129–145.

Lelek, A., and W. Tobias. 1982. Ergebnisse einer limnologisch-fischereibiologischen Exkursion auf dem Main unterhalb des Frankfurter Stadtgebietes. Natur und Museum 112(3): 87–93.

Leuthner, F. 1877. Die Mittelrheinische Fischfauna mit besonderer Berücksichtigung des Rheins bei Basel. H. Georg's Verl., Basel-Genf-Lyon.

Malle, K.G. 1983. Der Rhein — Modell für den Gewässerschutz. Spektrum der Wissenschaft (Scientific American in German language) 8: 22–32.

Meinert, W. 1985. Fischbewegungen zwischen Rhein bzw. Altrhein und blind endenden Seitengewässern. Ph.D. Thesis, Univ. of Mainz 285 p.

Melsheimer. 1878. Über bei Linz im Rheine gefangene Fische. Verh. naturh. Ver. preuss. Rheinl. Westph., Bonn. 35, Corr. Bl.: 95–98.

Meyer-Waarden, P.F. [ed.] 1965, 1966, 1967. Die Aalwirtschaft in der Bundesrepublik Deutschland - Wege zu ihrer Intensivierung. Arch. Fischwiss., 15, 16, 17(1): 1–130; 131–275; 277–494.

1972. Stephan Ludwig Jakobi, Begründer der künstlichen Besamung in der Fischzucht. H.E. Heenemann, Berlin.

Nau, B.S. 1787. Oekonomische Naturgeschichte der Fische in der Gegend um Mainz, Mainz. 120 p. —Im Schillerschen Verlage.

Peeters, J.C.H. and W.J. WOLFF. 1973. Macrobenthos and fishes of the rivers Meuse and Rhine, the Netherlands. Hydrobiol. Bull. Amsterdam 7: 121–126.

Pelz, G.R. 1985. Fischbewegungen über verschiedene Fischpässe am Beispiel der Mosel. Cour. Forsch.- Inst. Senckenberg, Frankfurt am Main. 76: 190 p.

Rosengarten, J. 1954 a. Der Aufstieg der Fische im Moselfishpass Koblenz im Frühjahr 1952 und 1953. Z. Fisch. Hilfswiss. III. N.F. p. 489–552.

Roth, J., and R. Kinzelbach, 1986. Der Status der Fischfauna des nördlichen Oberrheins im Jahre 1985. (Unpublished rep., Zool. Inst. of the Technical Univ. in Darmstadt, 17 p.).

Sanders, H. 1781. Beiträge zur Naturgeschichte der Fische im Rhein. Naturforscher. 15: 163–183, Berlin.

Schäfer, W. 1973. Altrhein-Verbund am nördlichen Oberrhein. Cour. Forsch.-Inst. Senckenberg 7: 63 p. Frankfurt am Main.

1978. Der Oberrhein, ökotechnisch gesehen. Cour. Forsch.-Inst. Senckenberg 31: 87 p. Frankfurt.

Schröder, T. 1979. Aspekte der Ökologie von Frühentwiklungsstadien einiger Fischarten in Altrhein und Labor. 100 p. M.Sc. thesis, Univ. of Frankfurt.

Siebold, C.T.E. von, 1863. Die Süsswasserfische von Mitteleuropa, Leipzig.

Stadler, H. 1961. Die Fische von Unterfranken, 84 p., Keller, Lohr a. Main.

Stambach, E. 1975. Die Wasserkraftnutzung am Rhein von den Quellen bis nach Basel. Special Issue of Wasser- und Energiewirtschaft 67(5–6): 168–177.

Steinmann, P. 1925. Die Lachsfischerei im Hochrhein. Schweizerische Fischerei-Zeitung 33: 26–27; 59–64: 81–87.

Thomas, E.A. 1975. Kampf dem zunehmenden Wasserpflanzenbewuchs in unseren Gewässern. Krautwucherungen als schwerwiegendes Gewässerschutzproblem in Fliessgewässern. Wasser und Energiewirtschaft Cours. d'eau et énergie 67 (1–2): 12–19.

Toivonen, J. 1972. The fish fauna and limnology of large oligotrophic glacial lakes in Europe (about 1800 A.D.). J. Fish. Res. Board Can. 29: 629–637.

Trahms, O.K. 1955. Der Rhein: Abwasserkanal oder Fischgewässer? Eine Betrachtung über die Fischereiverhältnisse im Rhein. Beiträge zur Rheinkunde 7: 43–56.

Vaas, K.F. 1968. Visfauna van het Estuariumgebied van Rijn en Maas. Biol. Jaarboek 36: 115–128.

Verhey, C.J. 1949. Het vorkommen van den steur (*Acipenser sturio*) in de mieuwe tuschen 1900 en 1931. De Levende Natur 52: 152–159.

Wijck, C.J.A. 1971. Onderzoek naar de visfauna in de omgeving van Nijmegen. Rep. Zool. Lab. Afd. Dierroecologie. Kath. Univ. Nijmegen, 40 p.

Wolff, W.J. 1976. The degradation of ecosystems in the Rhine, p. 169–188. *In*: The breakdown and restoration of ecosystems. Plenum Press, New York, NY.

Zschokke, F. 1919. Der Rhein als Bahn und als Schranke der Tierverbreitung. Verh. naturf. Ges. Basel 30: 137–188.

1931. Der Rhein, sein Lebensraum, sein Schicksal. 1. Bd., 3. Buch. Berlin-Grunewald.

The Fish and Fisheries in the Vistula River and its Tributary, the Pilica River

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Abstract

BACKIEL, T., AND T. PENCZAK. 1989. The fish and fisheries in the Vistula River and its tributary, the Pilica River, p. 488–503. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The Vistula River, Poland, has been channelized with levees, and vertical and longitudinal dykes. Most storage reservoirs have been built on its tributaries, but few on the Vistula itself. Pollution in the Vistula has increased dramatically since the 1950's, but decreased over the last decade in the Pilica River which has retained its natural character. The diverse habitats in the Vistula support an abundance of resident fish, but the Pilica is rather poor in fish. Harvests by commercial fisheries in the Vistula have declined and species composition has changed through a substantial decrease in numbers of migratory fish. The sea trout fishery is dependant on stocking. The sport fishery has increased. Barbel, chub, and dace in the Pilica reacted to improvement of water quality by extending their ranges upstream.

Résumé

BACKIEL, T., AND T. PENCZAK. 1989. The fish and fisheries in the Vistula River and its tributary, the Pilica River, p. 488–503. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Le cours de la Vistule, en Pologne, a été contenu par la construction de levées et de digues dans le sens du courant et en travers. La plupart des ouvrages de retenue ont été construits sur les tributaires, mais peu l'ont été sur la Vistule même. Dans cette rivière, la pollution s'est considérablement accrue depuis les années 50, mais elle a diminué ces dix dernières années dans la Pilica, qui a conservé son caractère naturel. Les différents habitats de la Vistule abritent d'importantes populations résidantes de poissons, mais la Pilica est assez peu poissonneuse. La récolte commerciale dans la Vistule est moins bonne qu'elle n'était et la composition spécifique a changé par suite d'une chute importante du nombre de poissons migrateurs. La pêche à la truite brune dépend du renouvellement des stocks. Il se fait plus de pêche sportive. Le barbeau, le mulet et le goujon de la Pilica ont réagi à l'amélioration de la qualité de l'eau en prolongeant leurs aires de distribution en direction amont.

Introduction

As early as the first Century A. D., the Roman commander Marcus Agrippa noted the river's name Vistula. Pomponius Mella (ca. 44 B.C.) produced a map of Europe on which, along with such rivers as Rhodanus, Rhenus, Albis (= Elbe in Germany), Ister (= Danube) there is the Vistula flowing north. Wulfstan, a 9th century sailor who travelled from England along the southern coasts of the Baltic, described the mouth of the Visle, "which is a large river" (Gierszewski 1982).

The river has always been important in the history of Poland, developing both a commercial and navigational role, with the establishment of many important towns including two Polish capitals — Cracow and Warsaw (from the 16th century). One of the main ports on the Baltic located in the delta is Gdansk, a city which grew in importance through foreign trade, mainly with rye, wheat, and timber transported down the river (Gierszewski 1982). Long rafts on the Vistula were a typical scene on the river until they practically disappeared after World War Two.

Gierszewski (1982) pays no attention to the fisheries, which may suggest a minor role in the country's economy. However, Gorzynski (1964) indicates that with the spread of Christian habits of fasting every Friday and before Christmas and Easter, fish have traditionally been important items of food.

In the early middle ages fishing rights belonged to the prince or king, who in turn conveyed them to high ranking clergy, monasteries, noblemen, towns or even villages with the conditions of supplying the Court with fish, usually the best kinds like salmon. (See Table 1 for common and scientific names of fish.)

Fishermen guilds or fraternities existed in may towns and had exclusive rights for fishing and fishmongering.

Some of these fraternities survived until the 20th century (Tobiasz 1962). Historians have noted conflicts between fishermen and raftsmen, the former who constructed fences and enclosures to catch and keep fish in rivers, and the latter for whom these barriers made navigation difficult.

TABLE 1. Scientific and common names of fishes mentioned or abbreviated in this paper.

Acipenseridae	
Sturgeon	*Acipenser sturio* L.
Salmonidae	
Atlantic salmon	*Salmo salar* L.
Sea trout	*Salmo trutta trutta* L.
Esocidae	
Pike	*Esox lucius* L.
Cyprinidae	
Roach	*Rutilus rutilus* (L.)
Dace	*Leuciscus leuciscus* (L.)
Chub	*Leuciscus cephalus* (L.)
Ide	*Leuciscus idus*(L.)
Asp	*Aspius aspius* (L.)
—	*Chondrostoma nasus* (L.)
Gudgeon	*Gobio gobio* (L.)
Barbel	*Barbus barbus* L.
Bleak	*Alburnus alburnus* (L.)
Silver bream	*Blicca bjoerkna* L.
Bream	*Abramis brama* (L.)
Vimba	*Vimba vimba* (L.)
—	*Pelecus cultratus* L.
Bitterling	*Rhodeus seriuceus amarus* (Bloch)
Siluridae	
Sheatfish	*Silurus glanis* L.
Anguillidae	
Eel	*Anguilla anguilla* (L.)
Gadidae	
Burbot	*Lota lota* (L.)
Percidae	
Zander	*Stizostedion lucioperca* (L.)
Perch	*Perca fluviatilus* L.
Cottidae	
Sculpin	*Cottus gobio* L.

The scope of this paper deals with the fisheries in the navigable part of the Vistula. But a river system is an entity and the main channel depends on its tributaries. Thus, for example, we shall describe the Pilica River, for which abundant data have been collected. As well, we discuss migratory fishes which reproduce in other Vistula tributaries but which are clearly affected by what has happened in the tributaries (Fig. 1).

Hydraulics, Morphometry, River Channel Modifications

The Vistula River rises at 1100 m a.s.l. and descends to 250 m a.s.l. along a short ca. 70 km stretch (Fig. 2). Thereafter it is a lowland river with gradients between 50 and 12 $cm \cdot km^{-1}$ in the upper and lower courses, respectively (Fig. 2). The Pilica River has a steeper slope (45 $cm \cdot km^{-1}$) but its source is only 348 m a.s.l. Therefore, its entire course is of lowland character. The Vistula basin covers much of Poland (Table 2) but the Pilica basin is only 4.8 % of that of the Vistula.

Average low and high water discharges of the Vistula are 320 and 4100 $m^3 \cdot s^{-1}$, respectively. The 13-fold difference between these values indicates a moderately irregular discharge within years; the Pilica River has a 20-fold difference. Although discharges in the rivers are of a snow-rainy type with usually one maximum and one minimum annually, the discharge from melting snow predominates. Spring floods are common when melting of snow and breaking of ice into ice-flows which sometimes accumulate at shallow places, contribute to a dangerous rise in water level (see Table 2). However, two of the most destructive floods ever recorded were in August 1813 and in July 1844 (Mikulski 1963).

Deforestation and development of agriculture has caused greater annual fluctuations of discharge. The quantitative effect of this change in the southern, sub-Carpathian part of the Vistula basin has been a drastic increase of the downcutting of the river beds (Klimek 1983). This erosion was greatest in the upper reaches of the Carpathian tributaries and imperceptible at the river's mouths. The downcutting rate had been maintained at between 1 and 1.5 $mm \cdot yr^{-1}$ over several thousand years but has increased this century. Between 1913 and 1947 (1955 in some rivers) it reached a rate of 10–33 $mm \cdot yr^{-1}$. From 1965 to 1975 the vertical erosion in these rivers was 30–90 $mm \cdot yr^{-1}$.

These changes have affected fish populations, at least by damaging the spawning grounds of salmon, sea trout, *Vimba vimba* and probably sturgeon.

Regulation of the Vistula River began in the 19th century but only at its end and during this century was any major progress achieved (Gierszewski 1982). The main works were the construction of levees along all stretches with low bordering land, the lining of banks with stone rip-rap and the erection of fascine groynes in order to narrow the river bed. The result was the disappearance of islands and braided reaches particularly in the lower course of the river. Three weirs with navigation locks (water level raised by 3.7–6 m) were installed in the upper Vistula between 1955–64. One dam also with locks was installed in the middle course (at Wloclawek in 1969) to aid navigation (Fig. 1). All of these have hydroelectric plants. Navigation conditions are not good (Fig. 2), which is why the river has minor significance in the country's transportation, less then 1 % of total tonnage (Piskozub 1982).

The Pilica River is considered navigable along the lowest 127 km of its course but may be used only by small barges up to 50 t (Kostrowicki 1968).

Major reservoirs aimed at flood control are located on southern tributaries of the Vistula (Fig. 1), none of which are older than 50 years. Sulejow Reservoir on the Pilica River was made by a 16 m high dam to supply water to Lodz City in 1974.

The most dramatic changes in the Vistula River bed occurred in the estuary. Before 1889 there were three main river branches but by 1915 a new river bed was made that flowed straight north and the three old branches were closed by dams or weirs (Mikulski 1963).

Unlike the Vistula, the Pilica River has retained its natural character except in the uppermost 20 km, the Sulejow Reservoir and in the lowest 10 km reach.

Feeding Grounds of Fish — River Bed Diversity

Regulation of the Vistula River with groynes has enhanced habitat diversity especially in the reaches where islands existed. Mikulski and Tarwid (1951) distinguished six types of bottom feeding grounds in the middle course of the river which differ with respect to water movement, kinds of deposits and, consequently, with regard to species composition and abundance of invertebrates. Sand covering

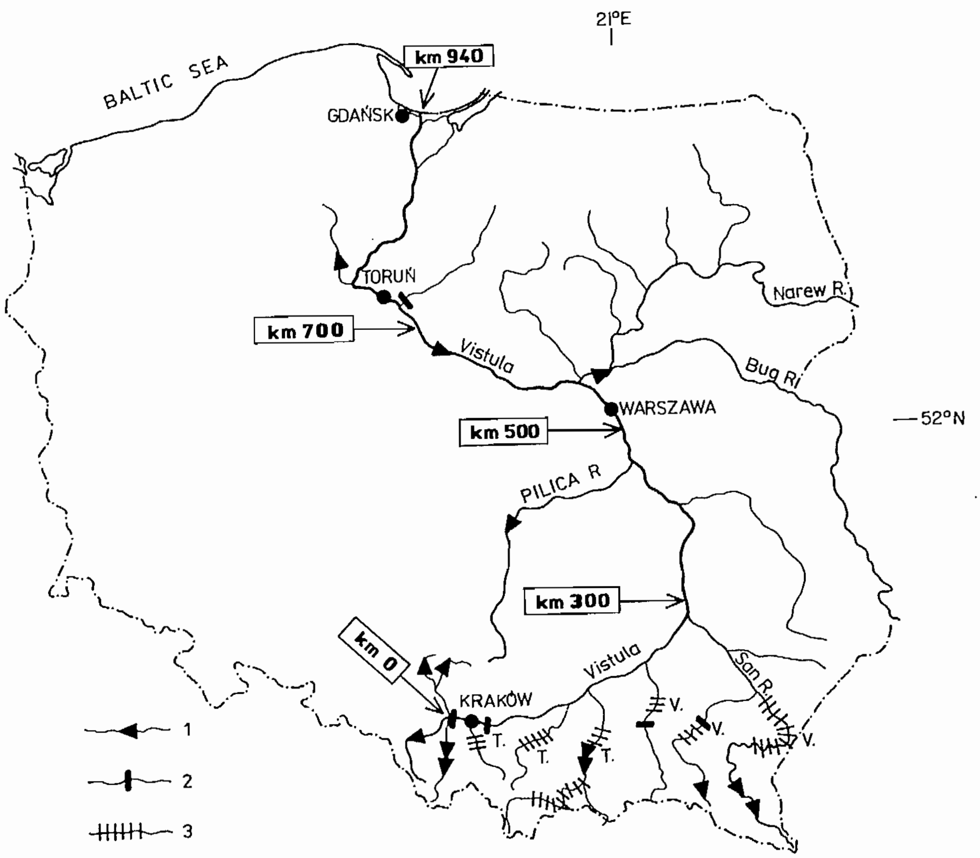

FIG. 1. Vistula River and its major tributaries. Dams (1) weirs (2) and main spawning grounds for sea trout (3, T) before 1940 and for *Vimba* (3, V) about 1960.

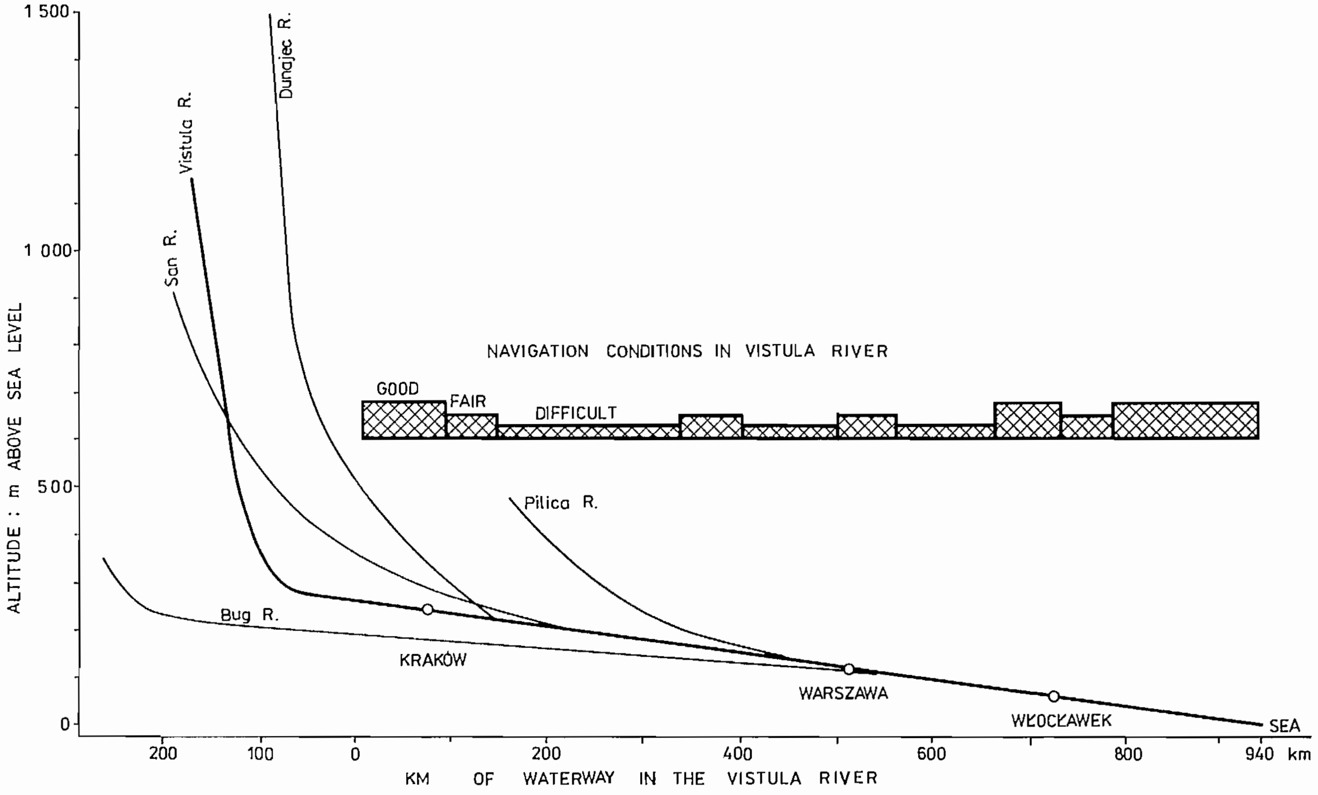

FIG. 2. Gradient profiles of the Vistula River and its major tributaries and navigation conditions along the main river (Piskozub 1982; Mikulski 1963).

TABLE 2. Selected data on the Vistula and Pilica rivers.

a) Vistula			
Drainage area	194 424 km^2 (equals 54 % of Poland's area)		
Total length	1 047 km (navigable length 941 km (see Fig. 1))		
Width of the river bed (navigable part) at:			
Km of length	Width (m)		
0-300	200-300		
300-600	500-1000		
600-675	water level raised by Wloclawek dam		
675-940	300-1000		
Annual precipitation on the drainage area (1980)	105.7 km^3		
Total annual discharge (of the whole river system)	33.0 km^3		
Slope:	0.50-0.12 m•km^{-1}		
b) Pilica River			
Drainage area	9 245 km^2 (equals 4.8 % of Vistula's drainage area)		
Total length	340 km (navigable length 127 km but for small units)		
Annual discharge	1.6 km^3 (equals 4.8 % of the Vistula River)		
Slope:	0.3-3.5 m•km^{-1}		
Width of the river bed:			
Km of length	Width (m)		
0-20	2-10		
20-170	10-50		
170-190	Sulejow Reservoir		
190-325	60-100		
325-335	30-45		
Water Temperatures (°C) (multiyear observations)	Minimum	Mean	Maximum
Spring (March, May)	0.1	8.1	22.8
Summer (June, Aug.)	12.1	18.6	25.9
Fall (Sept., Nov.)	0.5	9.8	22.2
Winter (Dec., Feb.)	0	1.3	6.5
Ice cover (multiyear average):	Beginning Dec. 20-Jan. 1		End Feb. 20-Apr. 10
Shore ice, floating ice floes etc. (multiyear average):	Nov. 10-31		Jan. 1-Apr. 31

Date from: Rocznik Statystyczny (Statistical Yearbook) for 1983 and Golek (1961) for temperature and ice phenomena.

most of the main stream bottom is a poor feeding ground when inhabited mainly by *Oligochaeta* but transitional muds, though ephemeral habitats, are very rich in food organisms, mainly *Chironomidae* with a large form of *Chironomus thummi*. Periodically flushed backwaters with deep mud deposits are also rich in *Chironomidae* but different forms (Kajak 1958).

Other habitats are inshore muds and open lentic waters e.g. between groynes, riffles and hard immobile objects such as fascine groynes exposed to current. The latter habitats are rich feeding grounds and typical organisms are the larvae of *Trichoptera* and *Simulium*.

Drift is an important source of fish food (Mikulski and Tarwid 1951). Zooseston, sampled in the main stream along the middle course of the river between 1955 to 1978, was dominated by Ciliata and Rotatoria, dramatically increasing in number (10-20 times) over the period. The numbers of Cladocera and Copepods were also much greater in 1977-78 than 20 years before (Praszkiewicz et al. 1983).

The contribution of the different habitats to the abundance of food for fish in the whole river has not been assessed. However, it seems obvious that reaches where habitat diversity is increased by existence of areas with much reduced current and many backwaters and hard objects, are richer than channelized reaches. Periodic freshets and floods enhance development of bottom food organisms. Transverse groynes which form partly lentic habitats connected with the main stream also increase food supplies for fish. Conversely, channelization, erection of weirs or dams and construction of reservoirs for flood control result in diminishing spatial and temporal diversity of river environments, and reduce the value of grounds for fish.

As mentioned above the Pilica River has remained a wild river along most of its course. In the strongly meandering channel one can distinguish four zones or habitats, which occur in a sequence in the river bed: (1) a pool or the deepest part at the concave bank with fast flowing current, (2) a shallow part at the opposite convex bank with slow current, (3) the middle zone between the above two with emerging sandy islands, (4) the transitional zone with sandy bottom, occasionally forming riffles. The first habitat contains the most abundant fishes: *Chondrostoma nasus*, *Barbus* sp., *Leuciscus* sp.; and shoals of bream, silver bream and roach occur in the slack water behind fallen trees. At the convex banks with a slow current there are piscivores, gudgeon and phytophilous cyprinids. On the shoals of the middle zone, fry of cyprinids and the piscivore *Aspius aspius* occur. The transitional zone is poorest for fish. Wherever the river banks are strengthened with stone and fascine, the density of fish, usually the small ones, is higher than in natural beds. Areas with highest fish abundance are near banks closely overgrown with willow (*Salix*) with overhanging and submerged twigs, -areas with high invertebrate densities.

Although information on the river bed configuration in the Vistula and Pilica rivers is not compatible, observations show that habitats in the middle course of the Vistula are much more diversified due to hydrotechnical constructions than are the habitats in the Pilica River. The positive role of stone and fascine embankments and dykes in the Vistula is confirmed by observations in the Pilica River.

Primary Production Versus Allochthonous Organic Matter

Rivers usually carry much more allochthonous than autochthonous matter (Webster et al. 1979; Vannote et al. 1980; Bott 1983; Welcomme 1979). We made a comparison of primary production with the organic matter in the drift for the middle course of the Pilica River (km 160). Primary production of phytoplankton dominated by diatoms was 2 888 kJ•m^{-2}•yr^{-1}, and respiration of algae was 14 % of gross production (Penczak et al. 1976b). Primary production was 4.5 times lower than in the Thames (Mann et al. 1972).

Macrophytes cover less than 1 % of the river bottom and contribute little to primary production. However, they constitute 15.2 % by weight of the total gut content of 9 fish species (Jakubowski 1975) and are important substrate for invertebrates.

The allochthonous matter was estimated as 25.1 J•m^{-3}, which gives a flow of organic matter through the studied site of 54 428 MJ•d^{-1} (Penczak et al. 1976b). Although these data are not directly comparable, one can infer that energy from allochthonous organic matter greatly exceeds that from autochthonous sources.

Pollution and Eutrophication

The most significant source of wastewater to the Vistula comes from industries and towns; in 1983, they contributed 23.2 % of the total annual discharge. Cooling water (15.1 % of total discharge) affects small stretches of the river, while other wastes, released at many places along the Vistula and its tributaries, strongly affect the entire course of the main river. The river is heavily polluted especially in its upper stretch (Table 3). Most indices of pollution have not changed since 1968 except an increase in soluble matter and chlorides (Dojlido and Wojciechowska 1983). Although these indices are very high, except for ammonia, they are not toxic to fish (Alabaster and Lloyd 1980).

Concentrations of heavy metals (zinc, copper, chromium, lead, cadmium, and nickel) (Dojlido and Taboryska 1983) showed high levels in the upper reaches near Cracow, and lower levels (except chromium) in the middle reaches. These concentrations exceed water quality criteria established for freshwater fish (Alabaster and Lloyd 1980; EIFAC 1983, 1984). The pollution of the Vistula River evolved with industrialization during the post-war period. In the late 1940's and early 1950's most of the river was unpolluted.

Along with the contamination of the river, there has been an increasing input of nutrients and organic matter resulting in eutrophication. Levels of phosphorus and nitrogen (ammonia in particular) have increased considerably over the last three decades, resulting in a substantial increase of phytoplankton (Fig. 3). Diatoms and green algae have always been dominant (Praszkiewicz et al. 1983). Thus, the level of primary production is high except, as in the upper Vistula, where it is reduced by high concentrations of heavy metals.

The Pilica River had been polluted mainly at three points: by a hardboard factory at km 62, by two factories and a town (Piotrkow Tryb.) at km 172 and by a town (Tomaszow Maz.) at km 209. These three sources contributed up to 89.8 % of the total pollution input into the Pilica River (Kleczkowski and Kowalski 1978; Banachowicz et al. 1980).

Together with the construction of the Sulejow Reservoir in 1974, purifying plants for the hardboard factory and Tomaszow Maz. were completed. Sewage has been directed, at km 172, to another drainage basin (Kleczkowski and Kowalski 1978; Banachowicz et al. 1980). The content of dissolved oxygen increased, oxydability decreased by 30 %, and the values of BOD_5 and the other indexes of pollution decreased even more (Table 3). Water quality gradually improved until 1984 in the middle and lower course of the river, but pollution has yet to be controlled in upper sections.

The development of agriculture has increased nutrient loads directly into tributaries and by surface runoff. From

TABLE 3. Selected water pollution indices calculated from monthly sampling at 45 sites along the Vistula River in 1978, and at 8 sites along the Pilica River in 1970–72 and in 1975–78. Data for Vistula from Dojlido and Wojciechowska (1983), and for Pilica River from Banachaowicz et al. (1980).

		Vistula (1978) (ranges of means)			Pilica (ranges)	
Item	Unit	Upper	Middle	Lower	1970–72	1975–78
BOD	mg O_2•L^{-1}	3.9 – 34.0	2.0 – 15.0	3.0 – 6.4	5 – 11	2 – 5
Oxygen	mg O_2•L^{-1}	3.6 – 9.5	9.3 – 10.5	8.0 – 11.1	6 – 9	9 – 11
Suspended matter	mg•L^{-1}	15 – 85	14 – 43	19 – 106	32 – 50	26 – 33
Dissolved substances	mg•L^{-1}	533 – 1416	384 – 607	321 – 489		
Chlorides	mg Cl•L^{-1}	86 – 636	94 – 144	39 – 80	10 – 33	11 – 38
Sulphates	mg SO_4•L^{-1}	78 – 144	54 – 103	44 – 74	85 – 183	66 – 116
pH		6.4 – 7.8	7.4 – 8.0	7.6 – 8.0	7.2 – 8.8	7.3 – 8.3
Ammonia	mg N•L^{-1}	0.5 – 3.2	0.5 – 1.3	0.3 – 2.5	1.2 – 2.8	1.2 – 3.9
Nitrates	mg N•L^{-1}	0.1 – 5.4	0.1 – 1.5	0 – 1.7		
Phosphates	mg P•L^{-1}		annual means below 0.5		0 – 0.4	0 – 1.8
(maxima)		0.8	0.7	1.8		

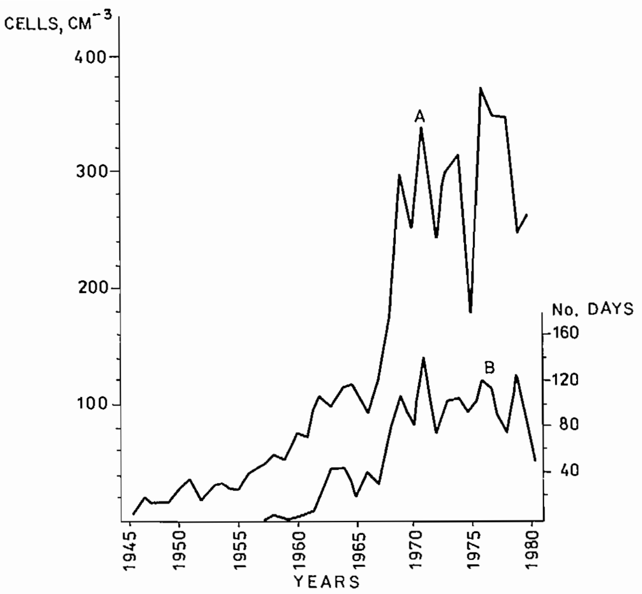

FIG. 3. Annual maxima of phytoplankton abundance (A) in 1000 cells•cm^{-3} and (B) numbers of days with abundance above 50 000 cells•cm^{-3} each year at water intake to the Warsaw filter station (modified from Praszkiewicz et al. 1983).

the drainage basin of the Pilica River about 2878 t of $N-NO^3$, 72 t $P-PO_4$ and 3581 t K move annually into the Vistula. Large amounts of nutrients carried by the Pilica influence the trophic state of the Sulejow Reservoir and cause troublesome blooms of algae (40–60 mg of biomass of phytoplankton L^{-1}).

Fishing and Sampling Fish in the Vistula River

Statistics of commercial fisheries in the Vistula are the only data on fish available for an extended period of time i.e. since 1952. These data are biased, however, because of quantities of fish not reported. Also they are biased with regard to the contribution of the most valuable species, which are often not recorded. The main fishing gear are drifting trammel and gill nets, the former prevailing in the middle and upper-lower courses, the latter near the mouth of the river. Mesh size (knot to knot) varies from 20 to 85 mm, the most frequently used ranging from ca 40 to 60 mm. Other fishing gear has also been used including drag nets, traps, and circular cast nets especially on riffles.

Between 1952 and 1955, juveniles and small fish were sampled with a tulle drag net (Backiel 1958) with a bag ca 2 m long, 1.5 m wide and ca 1 m deep and two 3 m long wings. The net operated in shallow lentic and moderately lotic habitats in the middle course of the river and caught small (1 to 7 cm) fish.

Another source of information on ichthyofauna was a collection of 6 piscivorous species: pike, zander, asp, perch, chub and sheatfish, 3634 individuals over the years 1954–57, from the Vistula between km 250 and km 852. This collection was used for the assessment of prey composition (Horoszewicz 1964) and for the estimation of growth, mortality, biomass, production and food consumption of these fish (Backiel 1971).

Two series of electrofishing, one in the upper course of the river (km 0 to 138) (Bieniarz and Epler 1972), and one in the middle course (km 367 to 459) (Nabialek 1984a) supplied information on fish living along banks. The latter series was carried out at nearly monthly intervals from 1973 to 1976 at 3–6 sites.

Finally, data on sport fishing were collected in 1971 and 1972 from questionnaires distributed by the Polish Anglers Association (Backiel 1983). The record from 693 questionnaires on fish caught did not distinguish the Vistula from other rivers, so the data should be treated with reservation. Another set of 93 questionnaires from 1979 concern the Vistula and adjacent waters (Leopold pers. comm.) but the proportions of recorded species are similar in both sets of data.

Fish Sampling in the Pilica River

Fish have been sampled in the Pilica River since 1965 using a D.C. electrofisher. Beklemishev's rule (Tarwid 1956) was used to determine the list and composition of species; that is the length (area) sampled was considered to be satisfactory if further sampling did not add to the species list. This rule was verified by us in the Pilica and Warta rivers and their various tributaries (Fig. 4). This kind of sampling differed depending on local conditions.

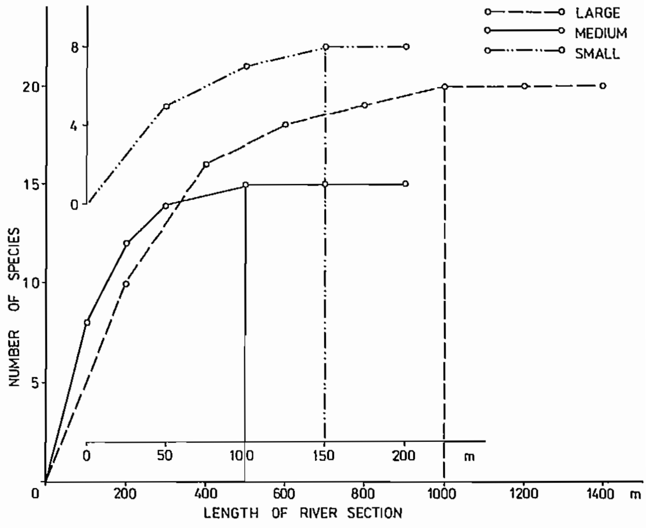

FIG. 4. The Beklemishev's rule for fish inventory sampling. Large — minimum section for sampling in river >40 m width, Medium — in river 10–40 m width, and Small — in river <10 m.

1. Large rivers. Width 40 to 100 m, mean depth in the current zone >1.0 m and slope <0.6 m•km^{-1}. While fishing from a drifting boat, the number of fish species did not increase after 1 km, a process which took about 30 minutes.
2. Medium rivers. Width 10–40 m, mean depth in the current zone >0.5 m and slope <1 m•km^{-1}; 15 minutes were necessary to drift along and electrofish a distance of 500 m.
3. Small rivers. Width <10 m, mean depth <0.5 m and slope <2 m•km^{-1}. Wading upstream with two anode dipnets, 150 m sections were fished to complete the list of species. (Penczak 1967).

Quantitative sampling in the Pilica River was based on the removal method of electrofishings (Leslie and Davis 1939), adapted by Penczak and Zalewski (1973, 1981), and Mann and Penczak (1984).

Fish Community — An Overview

Anadromous fish, are most intensively fished at the mouth of the Vistula and in their main spawning grounds are located in southern tributaries (Fig. 1); these species will be dealt with separately.

The other species do not undertake major migrations. Tagging experiments (Nabialek 1984b) suggested that the fish form "local populations". Differences in the growth of zander, perch and chub (Backiel 1971) between the upper reaches of the middle Vistula and the lower course showed small home ranges for these species.

The resident ichthyofauna of the Vistula consists of only 32 species. Data in Fig. 5 illustrate difficulties in assessing the composition of the whole fish community in a large river. One can, however, obtain valid answers to somewhat limited questions: what is the species composition of small fish, what are the proportions of fish exploited by piscivores and by men etc.?

Some characteristics of the fish community can be inferred from the data in Fig. 5. In samples from the tulle drag net, i.e. among small fish in shallows (column I), among the prey of piscivores, and in electrofishing catches the same five species, dominated by bleak, were found. Only two of them, roach and silver bream, are significant components of commercial and sport fishing.

In commercial catches the bream is dominant, whereas in sport catches more species are recorded and their contributions to the total are more evenly distributed. There is also a striking difference between species composition in commercial catches and in electrofishing (Fig. 5, columns III and IV) but the latter operates in the inshore habitats only and the former in the middle of the river channel.

Four species are considered typically fluvial: dace, chub, *Chondrostoma nasus* and asp but these species are not dominant except among the juveniles and small fish occurring in the lotic shallow habitats (Fig. 5, column I, *Leuciscus leuciscus*). Finally, the fish community is characterized by the presence of six piscivores.

However, this description of the fish community in the Vistula should be treated with caution because drastic changes occurred during the past three decades as reflected in commercial catches (Fig. 6).

In the Pilica River, inventory electrofishings were conducted first in 1965 at 44 sites in its middle course (between kilometre 70–260, Penczak 1968). In 1969–70 the whole drainage basin was investigated using similar methods and fishing equipment. In the main channel, 36 taxa were recorded (Penczak 1964) (Fig. 7). In the upper reaches, (first 60 km of the river) roach, bleak, gudgeon, and dace

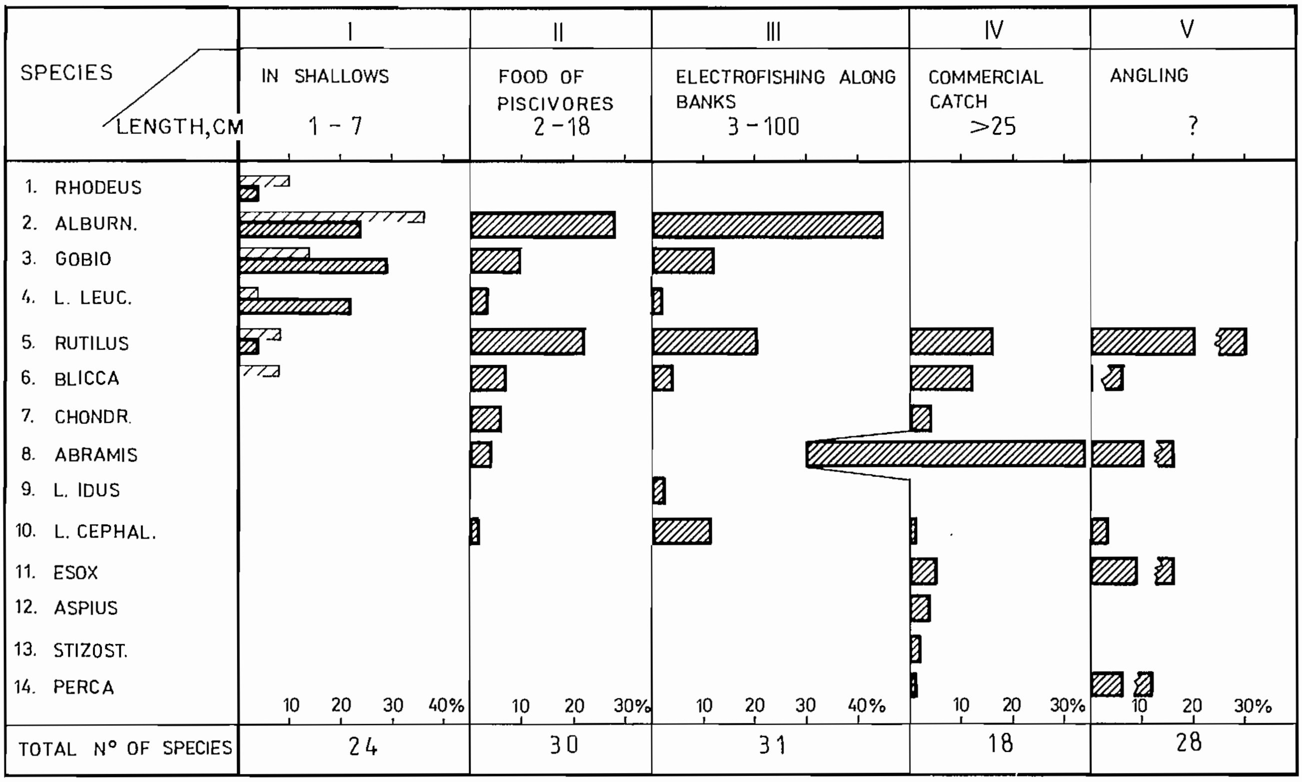

FIG. 5. Species composition of fish in the middle course of the Vistula River estimated by various methods. Share of 1 % or less not marked, migratory fish excluded, body length of captured fish indicated. I — data of Backiel (1958), upper bar-lentic, lower bar — lotic habitats, II — data of Horoszewicz (1964), recalculated, III — data of Nabialek (1984a). I, II, and III — percent of numbers, IV — commercial catches, mean from 1954 to 1968, upper Vistula excluded, V — angling from two sets of questionnaires on angling — ranges indicated. IV and V — percent of weight.

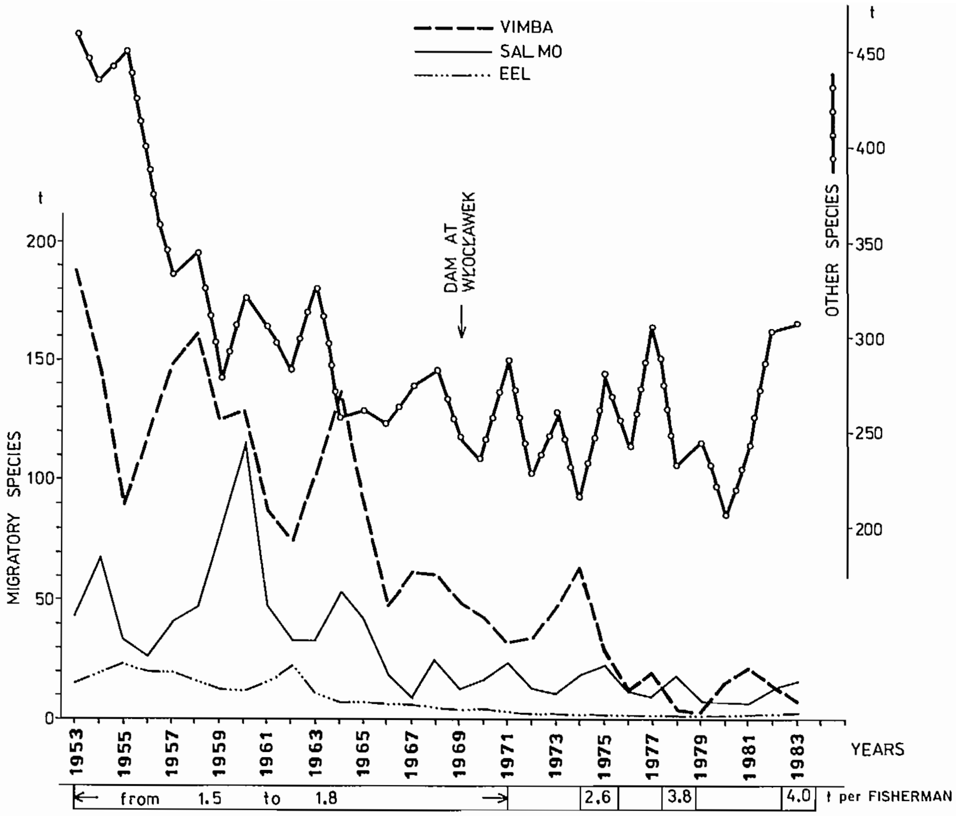

FIG. 6. Commercial catches in the Vistula River: sea trout, *Vimba vimba*, eel and all other species shown separately.

dominated. In the middle and lower courses above the Sulejow Reservoir, bleak, roach and chub were the most abundant, as in the Vistula (Fig. 5). The subdominant species, gudgeon, dace and chub are also similar in abundance with those in the Vistula.

The diet of piscivores (Jakubowski 1975) consisted of roach 25 %, pike 14 %, silver bream 12 %, gudgeon 11 %, chub 10 %, dace 9 %, burbot 8 %, sculpin 4 %, perch 2 %, and other species. Bleak, which was the dominant species at that time, constituted only 1.16 % of the fish biomass consumed by predators. This diet of piscivores in the Pilica differs from that in the Vistula where bleak dominated and cannibalism was negligible. The results of electrofishing and food analyses roughly corresponded with the abundance of roach, chub, gudgeon, and dace. The discrepancy between the contribution to the piscivore diet and the relative abundance in the Pilica with regard to bleak, silver bream and pike resulted from the fact that the piscivores were sampled mainly at sites with much reduced current and also from biases created through different capture methods.

Fisheries — General Consideration

The commercial fishery in the Vistula River (Fig. 6), is operated by professional fishermen who organized into cooperatives during the early 1950's. There were about 350 registered fishermen spread along the entire navigable course of the Vistula in 1952–55. Their numbers fell to 260 in 1964 and have decreased to about 60 at present; the numbers reported vary from year to year and some of the fishermen are said to work part-time. Until about 1970 the annual catch per fisherman was between 1.5 and 1.8 $t \cdot yr^{-1}$. The sharp decline of the professional fishery results from industrialization of the country along with a marked increase in urban population.

Working in river fisheries is less attractive in relation to the jobs in industry; as well increasing pollution has markedly affected fish production. Decline of migratory sea trout and *Vimba vimba* populations has made the fishery even less attractive. Conversely, sport fishing has rapidly developed. In 1955 there were 111 000 registered anglers in Poland, in 1972 the number was 413 000 and in 1986 it approached one million.

In spite of these trends, the annual catches of non-migratory fish by the commercial fishery has been near steady since about 1964 (Fig. 6). As shown in Fig. 5 the bream has been dominant and its annual catch has even increased, whereas the contribution of pike, zander and eel has diminished. Taking into account the catches per fisherman which have increased along with the decline of fisheries for migrants, one can infer that the biomass of catchable non-migrants has increased over the past 20 years at least by a factor of 2.

There is no commercial fishery in the Pilica River but casual observation indicates intensive sport fishing (Mann and Penczak 1984).

Effect of Pollution on Fisheries and Fish

The increasing pollution of the upper Vistula is reflected in its fisheries. The bad flavour of fish was noticed in the late 1950's. Electrofishing at 60 sites along the upper

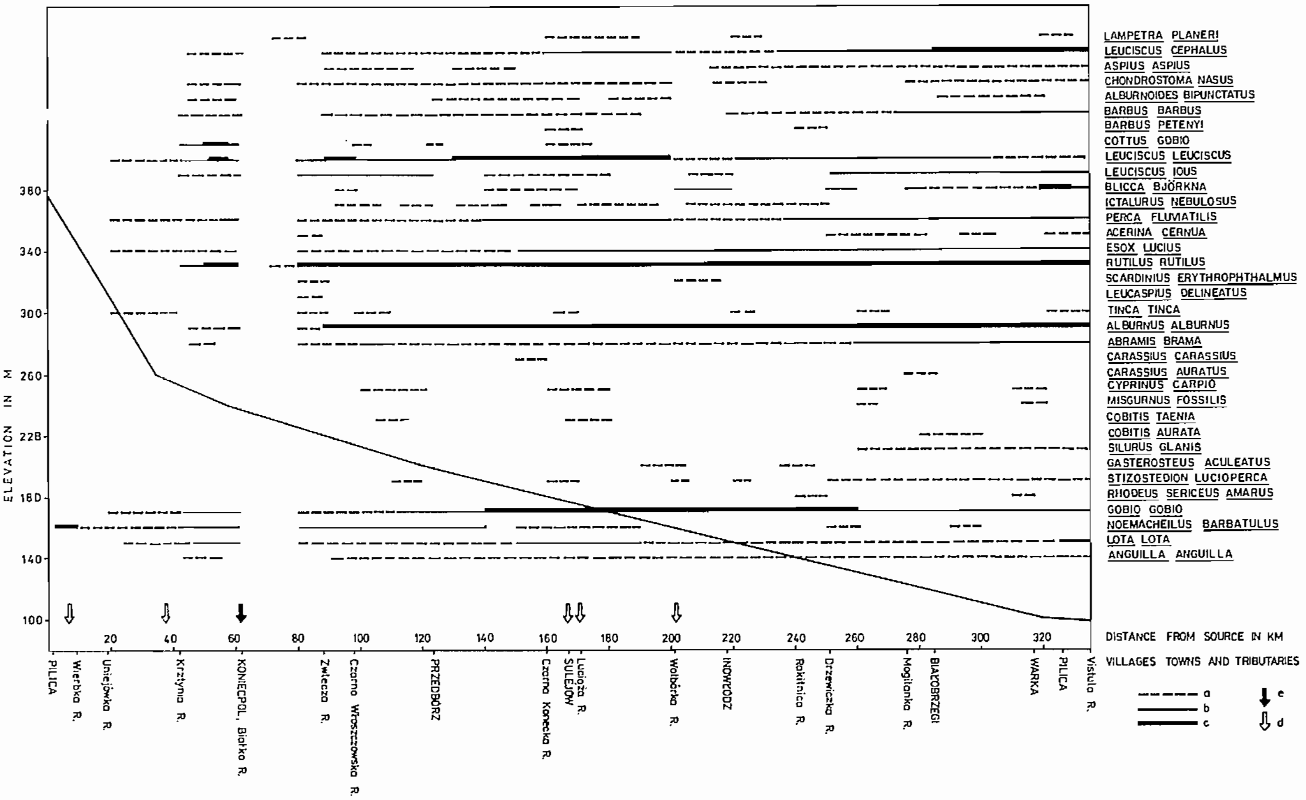

FIG. 7. Fish species distribution in the Pilica River in 1969–70. Below the abscissa names of towns, villages (large letters) and tributaries (small letters) are drawn. Fish caught within a given section are marked by lines, and their various thicknesses denote the species dominance in similar electrofishing conditions (Fig. 4): a — very abundant, b — abundant, c — rare; d — heavy pollution, e — medium pollution (see Table 2).

navigable stretch (km 0 to 138), (Table 3) in 1964–67 showed that a number of sites are practically fishless and only in the vicinity of tributaries were a few fish captured. The mean quantities of fish per 1 km of river bank were significantly smaller than those captured by a similar method in the middle course of the river where a similar species composition was found (Table 4).

Total mercury content in fish flesh from clean waters ranged between 0.006 and 0.16 mg•kg^{-1} while in the upper Vistula it was between 0.65 and 1.30 mg•kg^{-1} (Studnicka 1977). In fish from the middle and lower stretches of the river mercury concentrations were lower but still much higher than in fish from clean waters.

A petrochemical plant located above the Wloclawek impoundment (above km 700) (Fig. 1), caused a repulsive smell and taste to fish captured below the plant as well as pathological changes in their organs (Backiel 1983; Morawska 1968). In addition migrating sea trout and *Vimba vimba* acquired bad flavours that made them inedible.

The extent to which eutrophication has affected fish populations is not clear. Commercial catches of non-migratory fish in the middle and lower course do not show any trend since ca 1962. Mean catches per fisherman have increased since 1970 (Fig. 6). Though no estimates have been made for Vistula sport fishing there has been a rapid increase in the number of registered anglers all over the country and, no doubt, the same trend applies to this river. Thus, it appears that the middle and lower courses of the river accommodate a fairly high abundance of local fish in spite of considerable pollution.

Inventory electrofishing on the middle course of the Pilica River conducted in 1965 can be compared with data obtained in 1984 (Penczak unpublished). Between these years water quality has improved (section 5).

In 1965, the dominant species were, in the sequence of their importance, bleak, dace, roach and gudgeon, but over 20 individuals of any of the above-mentioned species in a 30 min electrofishing were only recorded as far downstream as the 95th–100th km of the river course (Fig. 8). In 1984, roach became the dominant species extending its range up to km 62. Dace has extended its range 25 km upstream, but downstream in the Sulejow Reservoir it is no longer abundant. *Chondrostoma nasus* has not been affected by the improvement in water quality, whereas chub and barbel have extended their range upstream by 30 and 80 km, respectively.

Barbel reacted similarly to the improvement in water quality downstream of the previously important source of pollution at km 209. The age of barbel caught in 1984 ranged from 1 to 6 years, with those of 1–4 years being dominant. This suggests that not only migration but also reproduction took place. On the other hand, the decrease in abundance and range of bleak in the purified Pilica is a surprise and no satisfactory explanation can be offered.

Density, Biomass, and Fish Production

Unlike the Pilica River where several experiments were made in order to estimate fish density and biomass (standing

TABLE 4. Percentage of dominant species in samples and total catch (in numbers) by electrofishing gear in the upper (after Bieniarz and Epler 1972) and in the middle Vistula River (after Nabialek 1984).

	Km 0 - 138 (1964–67)			Km 367–459 (1972–76)			
Species	Upper	Middle	Lower	I	II	III	IV[a]
L. cephalus	40.7	35.5	64.4	9.8	13.1	11.2	4.7
A. alburnus	24.6	28.9	7.4	43.5	52.3	42.0	44.1
R. rutilus	14.3	10.5	6.4	31.5	20.6	30.8	18.5
A. brama	2.8	7.7	5.8	x	x	x	x
C. nasus	3.0	2.0	4.8	x	x	x	x
G. gobio	x[b]	x	x	7.6	5.1	5.5	12.2
B. bjoerkna	x	x	x	x	3.5	x	4.1
Total %	85.4	84.6	88.8	92.4	94.6	90.1	83.6
Number of other species	14	18	14	14	20	24	22
Mean % of other species in sample	1.04	0.86	0.80	0.54	0.27	0.40	0.75
Number of fish per 1 km of the river bank	56	33	40	(from 200 to 6000 (most frequent range 600–2500))			

[a] — Four groups of sampling sites (summer samples only).

[b]x — Occurs in small quantities, included in "other species".

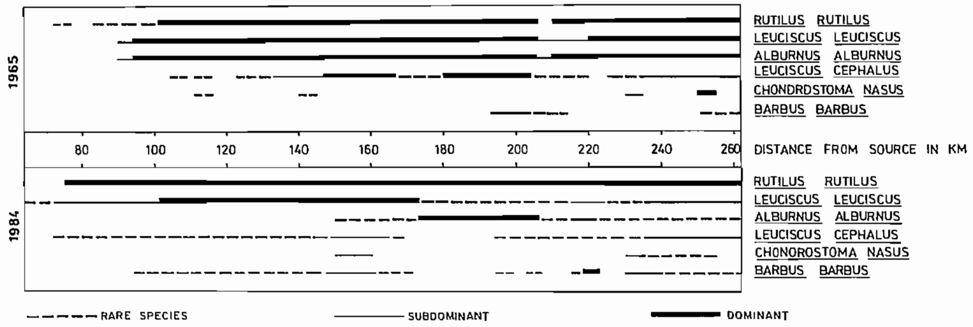

FIG. 8. The occurrence of species of fish in the middle course of the Pilica River in 1965 and 1984.

crop), no such data are available for the Vistula River. The only comparable figures are those from electrofishing at two reaches in the Vistula.

Successive fishing methods estimated fish density and biomass in several sites of the Pilica River (Table 5), ranging from 200 to nearly 1000 individuals•ha^{-1} and 10 to 130 kg•ha^{-1}, respectively. For a lowland medium size river, width from 40 to 70 m, the figures are low (Welcomme 1985).

Results of electrofishing in the Vistula — fishing along banks at selected sites — are presented as numbers of individuals per 1 km of the river bank (Table 4). Assuming the width of the fished section is 5 m, the area was 0.5 ha and from such areas in the middle course of the Vistula usually 600–2500 individuals i.e. ca 1200 to 5000 indiv•ha^{-1} were caught in a single fishing.

Electrofishing in a wide and deep river like the Vistula was less efficient than in the Pilica River where catch efficiency was usually more than 60 % compared with less than 30 % in the Vistula (Nabialek pers. commun.). Thus, there were probably nearly 10 times more fish in the middle Vistula than in the Pilica River. In the heavily polluted upper Vistula, fish density must have been much lower or negligible (Table 4).

Estimates of P/B ratio for roach (0.79–1.14), dace (0.47–0.61), chub (0.48–0.81), and for pike (1.14–2.50) in the Pilica varied from site to site mainly due to differences in the age composition of these populations (Penczak et al. 1976a, 1977, 1978; Mann and Penczak 1984). The P/B ratios for chub (0.37) and for pike (0.64–0.70) in the Vistula (Backiel 1971) are lower than that in the Pilica where only young age groups, especially pike, were present. The higher P/B values do not result in higher production in the Pilica than in the Vistula because of a much smaller biomass in the former than in the latter.

The partitioning of energy by fish populations in the two rivers allows some speculation on fish community performance (Table 6).

It is tempting to speculate about quantities in the food web of fish in the Vistula. The points of departure are with estimates for piscivores (Backiel 1971) and likely with yield. The figures for yield in the Vistula between 1952 and 1958 (total 13.4 kg•ha^{-1} and 1.9 kg•ha^{-1} of piscivores) were underestimated because sport fishing catches were included

TABLE 5. Estimates of fish quantities in the Pilica River obtained from successive electrofishing.

Site[a]		Site	Harvest	
# Location		Characteristic	N•ha^{-1}	Kg•ha^{-1}
1. km 161	a	concave bank	660	15.5
	b	concave bank	609	74.6
	c	concave bank	692	130.7
	d	convex bank	245	50.0
2. km 205		not polluted	997	22.4
km 209		polluted	206	10.6
3. km 158		—	200	11.7

[a] Site 1. — each site 0.2 ha, enclosed by fyke nets.
Site 2. — each site 0.35 ha, not enclosed by fyke nets.
Site 3. — three machines fishing simultaneously towards an electric barrier

Data from Penczak and Zalewski (1973, 1981); Mann and Penczak (1984).

and fishermen did not report all their catches. Later accounts of tag returns (Backiel 1983) and data from questionnaires from anglers indicate that the yield could be twice that recorded, i.e. 3.0 for piscivores and 26.8 kg•ha^{-1} for total yield (Table 7).

The "guesstimates" in Table 7 seem rather conservative for small fish. Among prey species, 50 % were species that grow to catchable sizes; therefore their production should not only cover predation but also recruitment to the catchable stock of non-predators and this was not taken into account. Thus, the total biomass is likely to be greater than 288.5 kg•ha^{-1}, much greater than estimates for the Pilica River.

Migratory Fishes

There were six migratory species in the Vistula River system: sturgeon, atlantic salmon, sea trout, two cyprinids (*Vimba vimba* and *Pelecus cultratus*), and eel. Walecki (1864) reported *P. cultratus* near Warsaw together with sturgeon in summer. But *P. cultratus* and sturgeon have never been numerous and became rare in the Vistula probably during this century. Sturgeon were reported as abundant in scattered historical accounts from the 13th to 17th centuries (Gorzynski 1964; Tobiasz 1962). Archeological excavations of layers dated at the 10–13th centuries in the estuary of the Vistula at Gdansk (Suslowska 1966; Urbanowicz 1965; Suslowska and Urbanowicz 1967) revealed a dominance of plates of sturgeon (bony plates) from among bones belonging to 19 species of fish. These findings suggest the intensive fishing for, and abundance of, fish in the Vistula estuary.

As late as the 19th century, sturgeon were common in the Vistula. At the Warsaw fish market sturgeon sold at low prices particularly in summer (Walecki 1864). About two decades later Nowicki (1889) complained that intensive fishing had made this species a rare fish in the upper Vistula. Sikorski (1899) confirmed this opinion. It is worth mentioning here that these authors agree about the relative scarcity of salmon and sea trout in the river.

At the turn of the century, the sturgeon fishery declined and after World War I few specimens were captured in any year from the lower Vistula. This rapid decline in the population was related to the profound changes of the river estuary and channelization of the main river bed (Backiel 1985). Although spawning grounds of this fish were not known, it is likely that the rapid increase of erosion of some rivers might have also affected the sturgeon. However, the scattered information on the fishery indicates overexploitation as another or jointly acting factor. The ban on fishing for sturgeon in the *Fisheries Act* in 1932 came too late to protect the species.

Records of catches of "salmon" in the upper Vistula and its tributaries during the second half of the 20th century (Kolder 1958) include both salmon and sea trout, but considering later reports the latter species was likely more abundant. Between 1953 and 1955 Jokiel (1958) collected 144 Atlantic salmon and 4000 sea trout; no reliable records of salmon have been available since then.

Unlike sturgeon, salmonid culture had already started by 1850 (Kolder 1958). Since 1879, the numbers of salmon and sea trout stocked and the contribution of fingerlings and smolts increased while that of fry decreased. These actions

TABLE 6. Energy flow through roach and dace populations in the Pilica River and through piscivore populations in the Vistula (in kJ•m^{-2}•yr^{-1}). Br — recruitment, C — consumption, P — production, Be — gonad production, F+U — excretion and faeces, R — respiration, Y — yield to man, Bm — biomass lost due to natural mortality

Sites	Species	Br	+	C	→	P	+	Be	+	FU	+	R
A) Pilica[a]												
1) km 205	Roach	0.004	+	27.34	→	2.51	+	0.25	+	5.48	+	19.09
	Dace	0.002	+	5.65	→	0.37	+	0.04	+	1.13	+	4.10
2) km 209	Roach	0.028	+	9.00	→	1.09	+	0.08	+	1.80	+	6.28
	Dace	0.146	+	8.12	→	0.58	+	0.13	+	1.63	+	5.90
B. Vistula[b] between km 300 and 870	6 piscivores	0.21	+	14.40	→	1.82	+	0.28	+	2.88	+	9.63
						↓						
						P	=	Y	+	Bm		
						1.82	=	0.80	+	1.02		

N.B. Site 1 — unpolluted, site 2 — polluted.

[a] Data from Penczak et al. (1977, 1978).

[b] Recalculated data from Backiel (1971).

TABLE 7. Estimates of production parameters of fish ($kg \cdot ha^{-1}$) in the Vistula River.

Trophic Level[a]	Yield Y	Production P	Consumption C	Biomass B
Exploited fish				
1. Piscivores	$Y_1= 3.0$	$P_1= 8.5$	$C_1= 68.4$	$B_1= 13.7$
2. Other species	$Y_2=23.0$	$P_2= 69.0$ $(3\times Y_2)$	$C_2=552.0$ $(8\times P_2)$	$B_2=138.0$ $(2\times P_2)$
Non-exploited small fish				
3. Prey of piscivores	$Y_3= 0$	$P_3=136.8$	$C_3=820.8$	$B_3=136.8$
Total	26.0	214.3	1372.8[b)]	288.5

[a] Piscivores — from Backiel (1971); parameters are doubled; Other species — parameters are based on the yield of level 2 (Y_2) and the ratios P_1/Y_1, C_1/P_1, B_1/P_1; Prey of piscivores — parameters based on consumption by piscivores (C_1) and pre-determined ratios (P/Y, C/P, B/P) for this level. e.g. $P_3=2\times C_1$, ie. production of small fish is twice the consumption by piscivores etc.

[b] Total consumption of invertebrates, plants, algae, detritus by level 2 and 3 fish.

did not help Atlantic salmon to survive, nor was there any correlation between stocked sea trout and subsequent catches. Increased catches in the Vistula (Fig. 6) up to 1960 could have resulted from stocking but may also be attributed to unknown changes in natural recruitment and in fishing. Subsequently, sea trout in the Vistula declined. Deterioration of water quality along with interruptions in the migration route were causes but fishing also had an adverse effect.

Damming the Vistula at Wloclawek in 1969 (Fig. 1, above km 700) has prevented sea trout from reaching the upper Vistula. The present sea trout fishery results from exploitation of adults in the sea and during spawning migration of stocks originating from stocking (Goryczko and Zielinski 1983; Sych 1980). This sea trout ranching has affected the trout's behavioural polymorphism because only the summer run fish have been collected for egg-taking, whereas the natural stock consisted of both summer and autumn runs, with the latter the larger. Now, however, the stock consists only of "summer run" sea trout.

As in the case of sea trout, fishing for *Vimba vimba* is concentrated in the lowest stretch of the Vistula. An extensive tagging program from 1960 to 1964 (Bontemps 1969; Backiel 1966) provided estimates of the annual fishing mortality coefficient (*F*) which ranged from 0.98 to 1.76 and was depensatory, i.e. greater when stock was large and vice-versa. Natural mortality (*M*) was 1.19. Thus, annual survival was 5.2 % when *Vimba vimba* entering the Vistula from the Bay of Gdansk was not abundant and rose to 11.5 % when its stock was about 3.5 times greater than in the former case.

These estimates apply to the period 1953-64 when catches were good although showing some downward trend. Since 1966 a drastic decline occurred (Fig. 6). Apart from the likely effects of overfishing it is quite possible that construction of two dams on the San River in 1960 and 1967 (Fig. 1) affected spawning and nursery grounds over a long stretch downstream. Another adverse effect could have been the rapid vertical erosion, especially after 1955, in the areas of rivers where most spawning grounds were located (Fig. 1).

Among migrating *Vimba vimba*, the age-groups VI and VII were strongly dominant, hence reproduction success in a certain year should be reflected in catches 6 and 7 years later. This time lag matches the time between hydroconstructions and diminished catches (Fig. 6). Similarly, the dam at Wloclawek in the lower river course, erected in 1969, prevented *Vimba vimba* from reaching spawning grounds in spring 1970, which in turn resulted in declining catches from 1976 to 1978. This dam, which has also affected sea trout migrations, has a fish-pass of the chamber type. Many individuals of 19 species actually entered the pass (Bontemps 1976) but the two upstream migrants have disappeared from catches above the dam since its erection.

In order to enhance the spawning of *Vimba vimba* fish were captured below the dam, transported and released into headwaters. From 1973 to 1975 the weights of *Vimba vimba* transferred in this way were 20, 10 and 14 tonnes, respectively, and the total catch of offspring of these fish was 57.2 tonnes from 1980 to 1983 inclusive. In 1978 and 1979 the catches below the dam were negligible (Fig. 6), thus, the transfers could be considered successful at least from the point of view of species conservation.

Conclusions, Perspective

Inventory and Assessment Methods

As described in section 7, in rivers in Central Poland up to 100 m wide electrofishing is a satisfactory method for conducting inventory research. A complete list of species may be obtained by increasing the length of the sampled section or by sampling in a small reach but in different seasons (Penczak and Zalewski 1981). When a river, such as the Vistula, is 200–1000 m wide, electrofishing also collected almost all species that inhabit the river. However, proportions of species in such fishings differ greatly from those in commercial and sport catches. Data in Fig. 5 suggest that this difference is related to size selectivity of fishing gear and to the distribution of species and size groups within the river channel. But what the true proportions are remains unknown.

Electrofishing alone usually is not satisfactory for an accurate assessment of density and standing crop in a river such as the Pilica, and even more so in a large river such as the middle Vistula. Good results in the Pilica were obtained by closing off portions of the river with nets, or by employing a higher than usual number of boats carrying electrofishing gear and limiting the escape of pelagic species by partitioning the river with an electric barrier (Mann and Penczak 1984). This latter method is efficient but expensive, hence we suggest using single catches obtained on several occasions, in which efficiency can be related to mean body weight of fish (Zalewski 1985). We have also shown that small fish are captured much less efficiently than large fish.

Among the navigable part of the Vistula, the commercial catches are the only source of information on long term trends in some catchable fish populations. This situation applies especially to migratory fish which seem to be very vulnerable to fishing by drifting gillnets and trammel nets. Sport fishing has grown considerably and will probably grow more in importance but only recently have studies began on this kind of fishing. Electrofishing in the Vistula has provided some qualitative and quantitative information. Also studies on the food consumption of piscivores can supply information on quantities of the small fish-prey of piscivores.

Impact of Human Activities

Four categories of human impact on rivers have been identified:

- land-use and ensuing erosion, in particular vertical erosion of river channels;
- pollution and eutrophication connected with the land-use;
- hydro constructions;
- fishing

Land-use changes and fishing affected the fisheries in the Vistula River system long before any major physical or chemical impact occurred. Physical habitat modifications together with waste disposal into the river system began during the industrial development in the 19th century, but their impact on fisheries became apparent only in this century, with particularly severe effects after World War II.

Welcomme's (1985) diagram showing development of catch as a function of fishing effort suggests effort is the main factor affecting catch up to a certain level after which abiotic factors become dominant. A plot of total catch and catch-per-fisherman versus numbers of fishermen in the Vistula in the past three decades apparently fits this generalization (Fig. 6 and 9). The resemblance may, however, be misleading because the number of fishermen drastically dropped over this period, fish became contaminated and

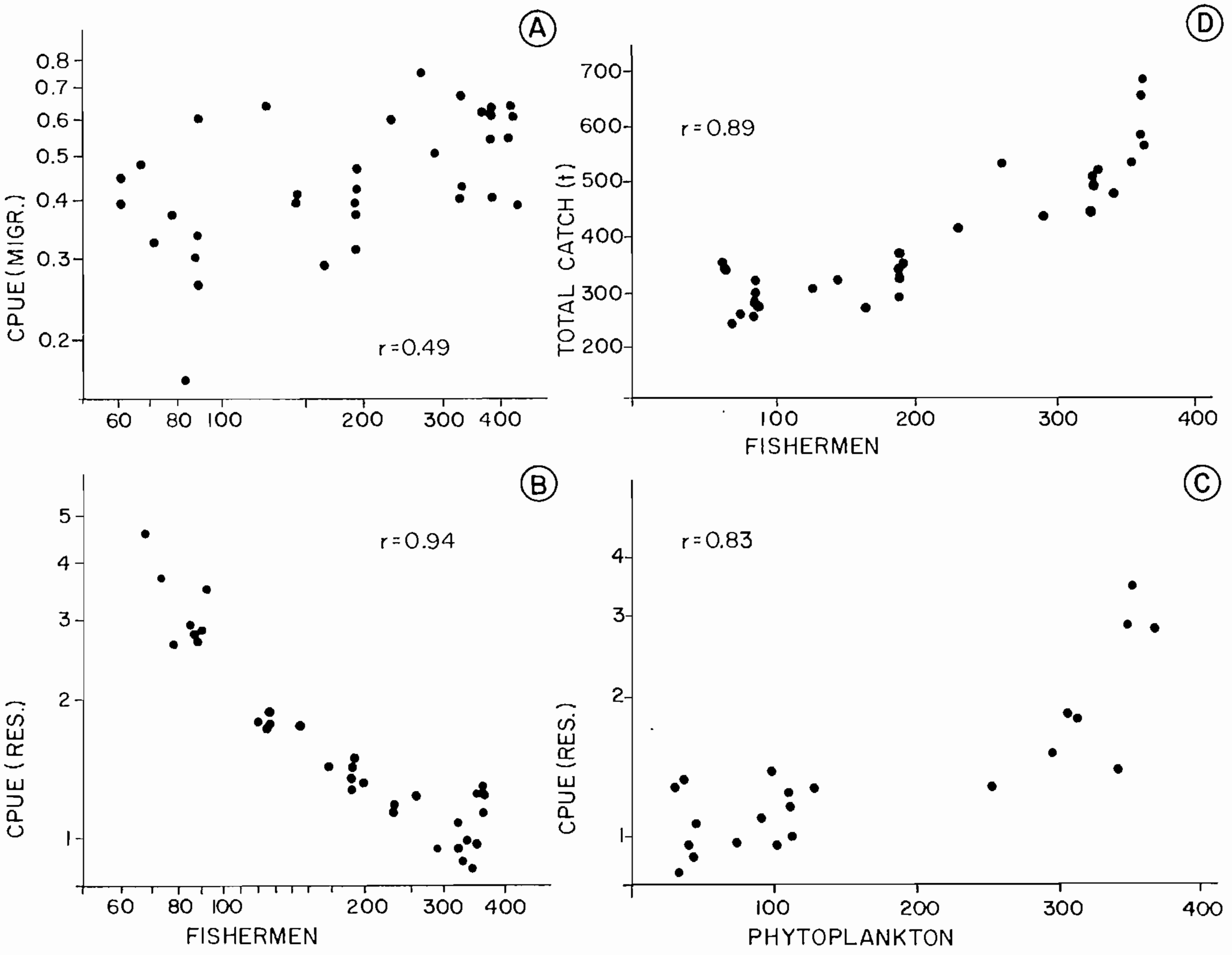

FIG. 9. Commercial fish catch in the Vistula River in 1953 through 1983. A — annual catch of migratory fish per fishermen — CPUE(MIGR) versus number of fishermen, log-log scale; B — catch of resident fish — CPUE(RES) vs. number of fishermen; C — CPUE(RES) versus maxima of phytoplankton from Fig. 3. r=correlation coefficients. D — Total catch vs. number of fishermen. Data on the number of fishermen (Wisniewolski 1984) missing for some periods were estimated by interpolation.

species diversity decreased due to regulation of the river channel and to dam constructions.

Most of the Vistula River system is at a developmental stage between "extensively modified" and "completely modified" (Welcomme 1985).

At this stage, fishing seems to exert little effect so that other factors are responsible for the degradation of fisheries. Such a situation is quite common to many river systems in industrialized regions (see Dodge 1989 and Fraser 1972).

Along with contamination, some enrichment in nutrients has occurred (Fig. 3) indicating increasing primary production. A plot of catch of resident fish per fisherman (CPUE (RES)) versus data on phytoplankton (Fig. 9) shows a positive correlation. But evidence was found that there are many fish in the middle course of the Vistula, although not healthy.

The Pilica is a good example of a slightly altered natural river, with numerous oxbow lakes, domination of forest and meadows in the catchment area, a small number of towns, only one reservoir, 300 m flood embankment, source section canalized, and the outlet section partly canalized. In spite of all these features the production of fish is low, probably because 86 % of the river bottom is of infertile sand, and thus offers few hiding and feeding places. However, old fishermen who used to fish in the middle and lower course of the Pilica between the First and Second World Wars recall that at that time barbel, *Chondrostoma nasus*, chub, bream and the now vanished *Vimba vimba*, formed abundant shoals, several times larger than those at present.

Intensive recreational fishing seems to be one of the major factors affecting abundance of fish. There is strong evidence (Penczak 1979) that when abundant populations of *Chondrostoma nasus* or barbel are discovered, they are fished until the last individual is captured; the situation has also been recorded for pike (Mann and Penczak 1984). When the bottom area of the concave bank (the area of the highest water velocity) is deserted by certain species, it is not recolonized by other species of fish living in the river (Penczak 1979). Thus contrary to the situation in the Vistula, fishing is a more important factor in the Pilica River.

An optimistic example of the effect of man's activity is the observed changes in fish occurrence in the Pilica River after some control of pollution was enacted (Fig. 8).

The middle course of the Vistula is rich in resident fish, which is probably related to the slower water current, a more diversified river bed and cultural eutrophication. Although sport fishing occurs, it is likely that because of the large size of the middle Vistula, fish are not so vulnerable to this activity as are fish in the Pilica River. The fish are also less attractive in this polluted river because of their tainted flavour.

Fisheries Management and Perspectives

Size limits for many species, total ban on catching some species, closed seasons and closed areas to enable undisturbed spawning and stocking rivers with quite a few species are ,fisheries management methods widely applied in Poland. Also fish passes have been constructed at several dams in the Vistula River system. Although there has not been any critical evaluation of these measures, except for stocking with sea-trout, it is clear that these steps have not prevented the drastic changes in fish communities and the subsequent decline of the Vistula fisheries.Urbanization and industrial development have had the major impact. Remembering the extreme examples, i.e. the almost fishless upper reach of the Vistula and relatively fast natural improvement of fish stocks in the Pilica River after an essential reduction of pollution, show that fishery management is helpless unless other users act for environmental protection.

The fishpass at Wloclawek on the Vistula did not prevent sharp reduction of migratory populations. However, ranching of sea trout replaced natural recruitment and this population is still commercially important. The other migrant, *Vimba vimba*, is likely to vanish unless either we help the population to pass the dam or the species forms a local land-locked population, something which has been observed in other river systems.

Unless water quality in the Vistula improves, any fishery management practice is a waste of effort and resources. There is, however, some hope for pollution control since there are many projects in the whole river system aimed at wastewater purification. There are also plans to build a number of dams and change the river into a cascade of impoundments. If these two processes occur the fish community will become still less diversified but production of the community will increase. These changes cannot be reversed by fishery management measures. Any attempt to restore the almost natural state of say, the 19th century would be futile. We must understand and envisaged the succession of events that will follow any major changes of water quality, of flow regime and river morphology. Then, considerations on fishery management should follow.

To this aim, multidisciplinary ecological research has already been undertaken in some river reaches and impoundments in the Vistula system. Accumulation of data on fish in impounded rivers has made it already possible to predict succession in the communities after dam construction (Backiel 1985).

There are no radical means of improving the 86 % infertile bottom area in the Pilica River, but dykes built of stones and other types of hiding places may significantly improve fish diversity and density (Swales and O'Hara 1983). Natural oxbow lakes constitute splendid hiding places and a source of food supply. In oxbow lakes 3–4 times higher density and standing crops were observed, and young fish were dominant there (Penczak and Zalewski 1974). Obviously the same applies to the Vistula, but all the oxbow lakes in its valley have been insulated behind levees. The regulation of current by means of groynes is beneficial for fish production.

For the Pilica River we strongly recommend that all available means be directed to habitat enhancement instead of stocking.

There is a great need for research on the effects of habitat modifications on fish communities. There is also need for critical evaluation of fishery management measures, especially in large rivers.

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References

Alabaster, J. S., and R. Lloyd. 1980. Water quality criteria for freshwater fish. Butterworths, London. 297 p.

Backiel T. 1958. Fry relations in shallow sectors of the middle Vistula River. Roczn. nauk roln. B 75: 313-362. (In Polish with English summary.)

1966. On the dynamics of an intensively exploited fish population. Verh. Int. Ver. Limnol. 16: 1237-1244.

1971. Production and food consumption of predatory fish in the Vistula River. J. Fish Biol. 3: 369-405.

1983. Fisheries and fishes of the Vistula River, p. 511-542. *In* Z. Kajak [ed.] Ecological Foundations of the management of the Vistula River and its basin. Polish Scientific Publishers, Warsaw (In Polish with English summary).

1985. Fall of migratory fish populations and changes in commercial fisheries in impounded rivers in Poland, p. 28-41. *In* J. S. Alabaster [ed.] Habitat modification and freshwater fisheries. Butterworths, London.

Banachowicz, T., J. Burchard, and H. Dubaniewicz. 1980. Trends in the purity of surface waters of the Pilica drainage basin. Studia Regionalne 4(9): 59-76. (In Polish).

Bieniarz, K., and P. Epler. 1972. Ichthyofauna of certain rivers in Southern Poland. Acta Hydrobiol. 14: 419-444. (In Polish with English summary).

Bontemps, S. 1969. Spawning migrations of *Vimba vimba* in the Vistula River. Roczn. nauk roln. H 90: 607-634 (In Polish with English summary).

1976. Migration des poissons au moyen d'une echelle de barrage sur la Vistule. Rev. Trav. Inst. Peches Marit. 40: 512-514.

Bott, T. L. 1983. Primary productivity in streams, p. 29-53. *In* J. R. Barnes and G. W. Minshall [ed.] Stream Ecology. Plenum Publishing Corporation, New York, London.

Dodge, D. P. [ed.] 1989. Proceedings of the International large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Dojlido, J. R., and J. Wojciechowska. 1983. Physico – chemical indices of Vistula River water pollution, p. 303-326. *In* Z. Kajak [ed.] Ecological Foundation of the management of the Vistula River and its tributaries. Polish Scientific Publishers, Warsaw, Lodz. (In Polish with English summary).

Dojlidio, J., and B. Taboryska. 1983. Micropollution of the Vistula River water and its tributaries, p. 327-351. *In* Z. Kajak [ed.] Ecological Foundation of the management of the Vistula River and its tributaries. Polish Scientific Publishers, Warsaw, Lodz (*In* Polish with English summary).

Eifac, Working Party on Water Quality Criteria for European Freshwater Fish. 1983. Report on chromium and freshwater fish. EIFAC Tech. Pap. 43: 31 p.

Eifac, Working Party on Water Quality Criteria for European Freshwater Fish. 1984. Report on nickel and freshwater fish. EIFAC Tech. Pap. 45: 20 p.

Fraser, J. C. 1972. Regulated discharge and the stream environment, p. 263-285. *In* R. T. Oglesby, C. A. Carbon, and J. A. McCann [ed.] River Ecology and Man. Academic Press, New York, London.

Gierszewski, S. 1982. The Vistula in the history of Poland fisheries. Wydawnictwo Morskie, Gdansk. 277 p. (In Polish with English summary).

Golek, J. 1961. Temperatures of Polish rivers. Prace Panstw. Inst. Hydrol. Meteorol. 62: 1-79 (In Polish with Russian and French summary).

Gorzynski, S. 1964. An outline of the history in ancient Poland. PWRiL, Warsaw. 89 p. (In Polish).

Goryczko, K., and Z. Zielinski. 1983. Result of sea trout smolt breeding in 1972-80. *In* Report 28th Meeting of Baltic Salmon Working Group. ICES. /M: 25, Appendix 11: 106-112.

Horoszewicz, L. 1964. Food of the predatory fishes in the Vistula River. Roczn. nauk roln. B 84: 293-314 (In Polish with English summary).

Jakubowski, H. 1975. Diet of predatory fishes in the Pilica River. Ph.D. thesis, University of Lodz, Lodz. 147 p. (In Polish).

Jokiel, J. 1958. Salmon, *Salmo salar* L., in the Vistula River. Roczn. nauk roln. B 73: 159-213 (In Polish with English summary).

Kajak Z. 1958. An attempt at interpreting the quantitative dynamics of benthic fauna in a chosen environment in the "Konfederatka" pool (old river bed) adjoining the Vistula. Ekol. pol. A6: 205-291. (Polish with English summary).

Kleczkowski, A. S., and J. Kowalski. 1978. Surface waters of the Pilica catchment basin. Studia Osrodka Dokumentacji Fizjograficznej. Polish Acad. Sci. 6: 51-70. (In Polish with English summary).

Klimek, K. 1983. Vertical erosion of the Vistula tributaries on the Carpathian foreland, p. 97-108. *In* Z. Kajak [ed.] Ecological foundations of the management of the Vistula River and its basin. Polish Sci. Publishers, Warsaw, Lodz. (In Polish with English summary).

Kolder, W. 1958. Stocking salmon and sea trout into the upper reaches of the Vistula River system in the years 1879 through 1954. Roczn. nauk roln. B 73: 216-267. (In Polish with English summary).

Kostrowicki, J. 1968. Physical Geography of Poland. Polish Scientific Publisher, Warsaw. (In Polish).

Leslie, P. H., and D. H. S. Davis. 1939. An attempt to determine the absolute number of rats on a given area. J. Anim. Ecol. 8: 94-113.

Mann, K. H., R. H. Britton, A. Kowalczewski, T. J. Lack, C. P. Mathews, and I. McDonald. 1972. Productivity and energy flow at all trophic levels in the River Thames, England, p. 579-596. *In* Z. Kajak, and A. Hilbricht-Ilkowska [ed.] Productivity problems of freshwaters. Polish Scientific Publisher, Warsaw, Cracow.

Mann, R. H. K., and T. Penczak. 1984. The efficiency of a new electrofishing technique in determining fish number in a large river in Central Poland. J. Fish. Biol. 24: 173-185.

Mikulski, Z. 1963. An outline of Poland's hydrography. Polish Scientific Publisher, Warsaw. 193 p. (In Polish).

Mikulski, J., and K. Tarwid. 1951. The probable influence of regulation of Vistula River bed on feeding grounds of fish. Roczn. nauk roln. 57: 179-204. (In Polish with English summary).

Morawska, B. 1968. Fish and fisheries in the Vistula near Wroclawek. Zesz. Nauk. SGGW, Zootechnika 7, Rybactwo 3: 23-56. (In Polish with English summary).

Nabialek, J. 1984a. The influence of heated effluents from the Kozienice thermal power plant on the shoreline Vistula ichthyofauna. Roczn. nauk roln. H 100: 83-109. (In Polish with English summary).

1984b. Translocations of fish in the region of effluents of heated water from the Kozienice power plant. Rocz. nauk roln. H 100: 71-82. (In Polish with English summary).

Nowicki, M. 1889. About the fishes of the drainage basins of the Vistula, Styr, Dniepr and Prut rivers in Galicia. Wyd. "Czasu" Fr. Kluczynskiego i Sp. Cracow. 54 p. (In Polish).

Penczak, T. 1964. Report on catching *Petromyzon marinus* L. in the River Pilica. Naturwissenschaften 13: 322 p.

1967. The biological and technical principles of fishing by use of direct-current field. Przeglad Zoologiczny 11: 114-131 (In Polish with English summary).

1968. The ichthyofauna of the rivers of the Lodz Upland and adjacent areas. Part Ib. The hydrography and fishes of the Pilica River basin. Acta Hydrobiol. 10: 499-524 (In Polish with English summary).

1979. Ecological fish production in Polish rivers. Proc. 1st Brit. Freshwater Fish. Conf., Liverpool, 1979, p. 11-29.

Penczak, T., M. Molinski, and M. Zalewski. 1976a. Production of pike, roach and chub in a selected fragment of Pilica River (barbel region). Polish Arch. Hydrobiol. 23: 139–153.

1976b. The contribution of autochthonous and allochthonous matter to the trophy of a river in the barbel region. Ekol. pol. 24: 113–121.

Penczak, T., and M. Zalewski. 1973. The efficiency of electrofishing with rectified pulsating current in the zones of a river of medium size, evaluated by the method of successive catches. Acta Hydrobiol. 15: 343–355.

1974. Distribution of fish numbers and biomass in barbel region of the river and the adjoining old river-beds. Ekol. pol. 22: 107–119.

1981. Qualitative and tentative quantitative estimates of the fish stock based on three successive electrofishings in the medium-sized Pilica River. Polish Arch. Hydrobiol. 28: 55–68.

Penczak, T., M. Zalewski, M. Molinski, and M. Gajos. 1977. The ecology of roach, *Rutilus rutilus* (L.), in the barbel region of the polluted Pilica River. IV. Elements of production and food consumption. Ekol. pol. 25: 241–255.

Penczak, T., M. Zalewski, and K. Pfeifer. 1978. Materials for the ecology of the dace, *Leuciscus leuciscus* (L.) from a polluted river in the region of the barbel (The Pilica River). 1. Production and food consumption. Acta Hydrobiol. 20: 63–85.

Piskozub, A. 1982. The Vistula — a monograph of the river. Wydawnictwo Komunikacji i Lacznosci Warsaw. 447 p. (In Polish).

Praszkiewicz, A., I. Spodniewska, and T. Weglenska. 1983. Seston of the Vistula River and reservoirs of the Vistula cascade of the reach from San River mouth to Wloclawei, p. 435–488. *In* Z Kasjak [ed.] Ecological Foundation of the management of the Vistula River and its tributaries. Polish Scientific Publisher, Warsaw, Lodz. (In Polish with English summary).

Sikorski, W. 1899. Fish farming. Druk W. Szulc, Warsaw. 467 p. (In Polish).

Studnicka, M. 1977. Investigation into the content in tissues and toxicity of mercury for fish. Acad. roln. Lublin, Seria-Rozprawy naukowe 47: 77 p. (In Polish).

Suslowska, W. 1966. Fish remains from the Prince's quarter of Gdanzk. Przeglad Zoologiczny 10: 198–203. (In Polish with English summary).

Suslowska, W., and K. Urbanowicz. 1967. Bone remains of fish from early medieval Gdansk (10th–13th centuries), p. 53–65. *In* J. Kaminska [ed.] Early medieval Gdansk, v. 6, Wyd. Ganskie Tow. Naukowe, Gdansk. (In Polish with English summary).

Swales, S., and K. O'Hara. 1983. A short-term study of the effect of a habitat improvement programme on the distribution and abundance of fish stocks in a small lowland river. Fish. Manage. 14: 135–144.

Sych, R. 1980. On the modelling of the Baltic salmon and sea trout stock exploitation. Report of the 27th Meeting of the Baltic Salmon Working Group. ICES, C. M. 1981/M:2, Appendix 3: 14–32.

Tarwid, K. 1956. Beklemishev's criterium of faunistic reliability of quantitative samples. Ekol. pol. B 2: 27–31 (In Polish).

Tobiasz, M. 1962. The fraternity of Cracow fishermen. Wyd. WSR, Olsztyn. 96 p. (In Polish).

Urbanowicz, K. 1965. Sturgeon fishings in the early medieval Gdansk in the light of archeological findings. Przeglad Zoologiczny 9: 372–377 (In Polish with English summary).

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

Walecki, A. 1864. Systematic review of local fishes. Druk, Gazety Polskiej, Warsaw. 115 p. (In Polish, first scientific and critical description of freshwater fishes in Poland).

Webster, J. R., E. F. Benfield, and J. Cairns, Jr. 1979. Model predictions of effects of impoundment on particulate organic matter transport in a river system, p. 339–364. *In* J. V. Ward and J. A. Stanford [ed.] The ecology of regulated streams. Plenum Press, New York. London.

Welcomme, R. L. 1979. Fisheries ecology of floodplain rivers, Longman, London. 317 p.

1985. River fisheries. FAO Fish. Tech. Pap. 262: 330 p.

Wisniewolski, W. 1986. Commercial catches of fish in the Vistula, Odra and Warta rivers. Roczn. nauk roln. (In Polish.) (In press)

Zalewski, M. 1985. The estimate of fish density and biomass in rivers on the basis of relationships between specimen size and efficiency of electrofishing. Fish. Res. 3: 147–155.

Present State of the Environment, Biota, and Fisheries of the Volga River[1]

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Abstract

PAVLOV, D.S., AND B. YA VILENKIN. 1989. Present state of the environment, biota, and fisheries of the Volga River, p. 504–514. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

The Volga River arose after the last glaciation to drain the Russian European Plain. It has long served as a major transport artery and recent engineering works have turned the river into a major link between the Baltic and Black Seas. The river and its major tributary, the Kama, are also used for hydroelectric power generation and irrigation and are impounded to form a cascade of large dams along their length. Characteristic changes have occurred in the biology of the river since impoundment with a shift from riverine to lacustrine characters. The fish community is complex with 74 species, some of which have been introduced or have penetrated the system from adjacent marine areas. The basin provides some half of the total inland water catch of the USSR and there is a high positive correlation between area and catch in the reservoirs. Fish populations are maintained by intensive management, including stocking, construction of fish passes and establishment of artificial spawning grounds. High negative correlations between replacement rate of water in the reservoirs and the fish catch have been noted.

Résumé

PAVLOV, D.S., AND B. YA VILENKIN. 1989. Present state of the environment, biota, and fisheries of the Volga River, p. 504–514. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Le fleuve Volga, né après la dernière glaciation, draine la plaine russo-européenne. Ayant longtemps servi de principale artère navigable, la Volga est devenue, grâce à de récents travaux d'ingénierie, un trait d'union important entre la Baltique et la mer Noire. Le fleuve et son affluent principal, la rivière Kama, servent également à la production d'hydro-électrieité et à l'irrigation. Leurs eaux sont retenues par un escalier de grands barrages construits sur leur cours. La vie du fleuve s'est profondément transformée depuis qu'il a été endigué et les caractéristiques de la biologie fluviale ont fait place à celles des lacs. La faune aquatique complexe comprend 74 espèces; certaines d'entre elles ont été introduites dans ce système ou y ont pénétré à partir des milieux avoisinants. Le bassin de la Volga fournit environ la moitié des prises intérieures totales de l'U.R.S.S. et on remarque une corrélation fortement positive entre la superficie des zones de pêche et les prises enregistrées dans les réservoirs. La stabilité des populations de poissons est assurée grâce à une gestion intensive faisant appel au stockage, à la construction de passes migratoires et à la création de frayères artificielles. On a observé des corrélations fortement négatives entre le taux de remplacement de l'eau dans les réservoirs et les prises de poisson.

History of the Basin

The present form of the Volga River basin emerged from a succession of glaciations between 700 000 and 10 000 yr ago. Glacial influences are particularly visible in the upper part of the basin where lakes and boulders are abundant. The postglacial history of the river has been affected by fluctuations in the level of the Caspian Sea arising from tectonic activity and long term differences in precipitation patterns. These events influenced the length of the lower part of the river, and the area and position of the delta, although the lower part of the basin was never glaciated.

Human interventions have modified the basin still further. The Vyshne–Volotzk canal, constructed in the early 18th century, connected the Tvertza River with tributaries of Lake Ladoga and thus the Baltic basin. This system is still in use but a further connection between the Volga system, the White Sea, and the Baltic was constructed in the early 19th century. Then, the Mariinsk canal was reconstructed in 1964 to take ships of up to 3 000 tons. Full communication between the Baltic, White, Caspian and Black seas started in 1933 with the opening of the White Sea–Baltic canal, and was completed in 1952 with the Volga–Don canal.

Location

The Volga River basin occupies the central part of the Great Russian plain although it also drains part of the western slope of the Ural highlands. The total catchment area

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[1] Information in this paper is valid only until the early 1980s.

of 1.36×10^6 km^2 represents about a quarter of the area of European USSR. The basin extends 1 910 km from north to south (61° 55' to 45° 35'N) and 1 805 km from east to west (32° 05' to 61° 22'E) (Fortunatov 1978).

The northern part of the basin is in a forested zone of southern taiga, mixed hardwood and softwood forests. In its course southwards the river successively crosses forest-steppe and semi-arid zones, and the arid Delta region.

Users

Voropaev and Velikhanov (1984) have described the present utilization of the basin. The Volga and Kama rivers are the main transport arteries between the Caspian, Azov, White and Baltic seas which handle some 350 million tons of shipping per year or about 70 % of the total river-borne shipping of the USSR.

The new Tcheboksar hydroelectric power plant will increase the total generating capacity of the Volga system to 11 300 megawatts giving an average annual output of 40 billion kilowatt hours. This output represents about 20 % of the energy demand of the central and Volga regions of the USSR. The plant is a principal contributor to peak power supply in the unified national energy system.

Water from the Volga irrigates 1 300 000 ha of agricultural land, with future increases in area planned. Water extraction for industrial and domestic purposes is small in comparison but still requires more than 30 km^3 year.

Major Stresses

Major stresses arise from water use. The regulation of the river and complete loss of abstracted waters have reduced annual flow by about 20 km^3 (Butorin and Monakov 1984). Recently, increasing quantities of water are being withdrawn from the Lower Volga and, although some water is lost, that which is returned is more highly mineralized. Some authors have suggested that the annual drainage of nutrients into the river from agricultural lands alone is between 30 000 and 500 000 t and as a result nitrogen and phosphorus content in the water exceeds natural levels by 2–3 times. Local variations and specific composition of nutrients depend on the use of surrounding lands. For example, greater nitrite concentrations occur in reservoirs located in agricultural areas. Water level fluctuations in reservoirs are as great as 6 m, making conditions unfavorable to many species of fish. Furthermore, the flow of 120 km^3 of water in April–June needed for the maintenance of the fisheries of the Lower Volga and Delta conflicts with demands for transportation and power generation (Voropaev and Velikhanov 1984). The reduced volume of water in the system resulting from water abstraction has further aggravated this conflict.

Some 25 km^3 of wastewater are discharged annually into the Volga basin, representing 10 percent of the average long term flow. Indications of pollution appeared early. Severe deoxygenation (to 0.5 mg $O_2 \bullet L^{-1}$) was recorded in the winters of 1939 and 1940 arising from paper mill effluents (Zhadin 1950). Navigation as well as discharge of industrial wastes have contributed to contamination by hydrocarbons (Butorin 1978). Indicators of eutrophication now appear stable (Nikanorov 1974) and water quality is generally high. However, serious local deterioration of water quality is indicated for some reaches of the river. As a measure of the quality of the water in the basin, the excellent drinking water of Moscow, obtained from the Volga through the Moscow–Volga canal, is mostly naturally purified in lakes which are protected from other water use.

Morphology

The Volga basin contains 151 000 rivers and streams of over 10 km in length (Fortunatov 1978). The Volga may be divided naturally into three portions (Fig. 1):

- The Upper Volga from the source to the River Sheksna confluence;
- The Middle Volga from River Sheksna to the Volzhsk dams;
- The Lower Volga from the dam to the Caspian Sea.
- The Delta is sometimes considered a separate area.

The river has, over the years, been converted into a cascade of large reservoirs whose characteristics are summarized in Table 1.

The source of the Volga River is in the Valdai hills at an altitude of 228 m a.s.l. The flow of the Upper basin was regulated by a dam built in 1843 and reconstructed 100 yr later. The Verkhnevolzhsk reservoir was formed above the dam, but downstream the channel falls away in a series of rapids to the Verkhnevolzhsk lowlands and the first cascade of three reservoirs. The Rybinsk, the basin area above the lowest of these, is 150 000 km^2.

The Middle Volga also contains a cascade of three reservoirs and is joined by the two major tributaries of the Dama and Oka rivers. The Kama itself is regulated by a cascade of three reservoirs. The basin area above the Kujbyshev reservoir is 1 221 000 km^2.

The Lower Volga includes two reservoirs and the river channel from below the Volgograd reservoir and the river mouth. Just below the reservoir the Volga divides into its main channel and the Akhtubinsk arm (603 km in length). The Volga valley, known as the Volga–Akhtubinsk floodplain, is transformed into the Delta 150 km upstream from the Caspian Sea.

The Delta, about 12 000 km^2, historically has been very unstable with numerous shifting channels and islands. The navigation channel has changed its position frequently during the last 200 yr.

The longitudinal section of the Volga and Kama rivers is shown in Fig. 2. The main channel length of the river has been shortened by the hydrological works of recent years from 3 690 to 3 530 km mainly by flooding of meanders.

Energy Flow

The species composition of dominant organisms at lower trophic levels in the river has changed significantly following water flow regulation because ecosystems have changed from riverine to characteristically lacustrine (Rivjer and Dzjuban 1978).

The annual average long-term values for phytoplankton biomass vary from 1.0 to 11.4 $g \bullet m^{-3}$ per whole volume in different reservoirs. The highest biomass occurs in reservoirs which are in the process of filling. Diatoms are more common than blue-green algae, indicating good water quality, although species composition has shifted from domi-

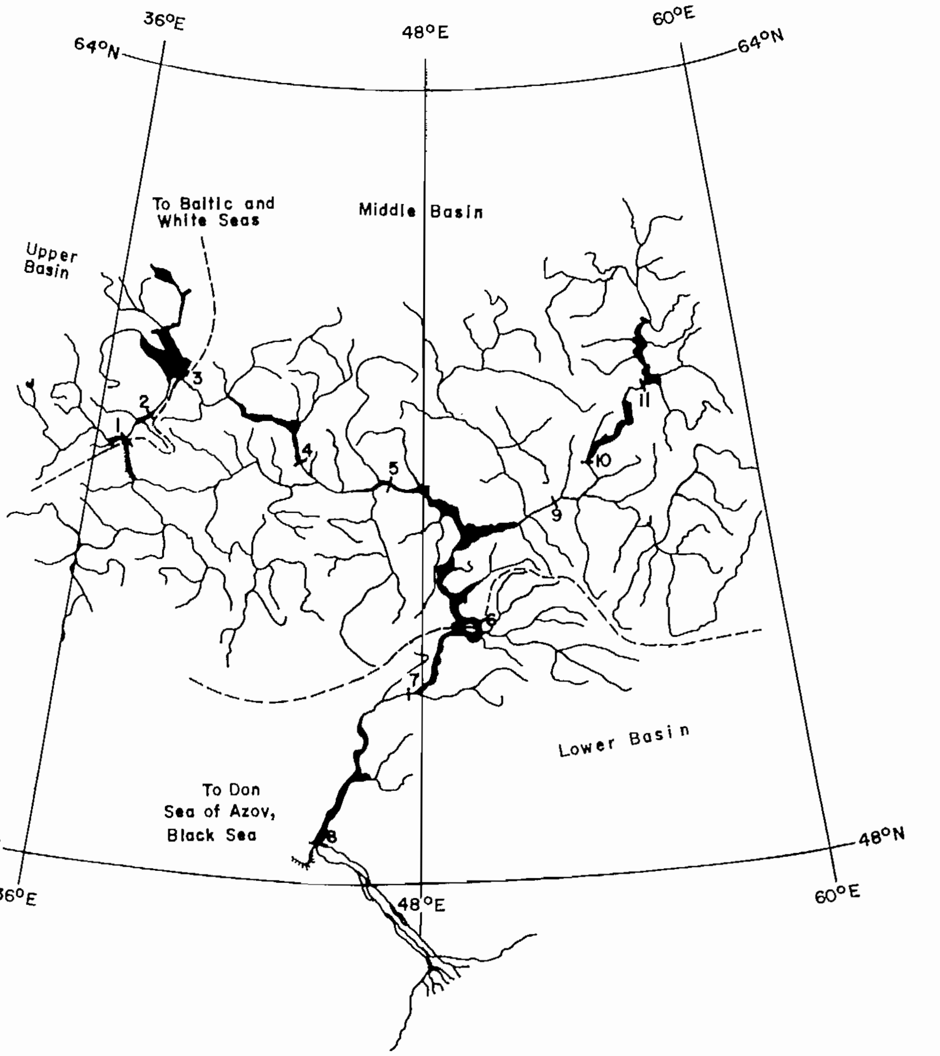

FIG. 1. The figures on the map denote the Volga (1–8) and Kama (9–11) dams and reservoirs. 1. Ivan'kov, 2. Uglitch, 3. Rybinsk, 4. Gorky, 5. Tcheboksar, 6. Kujbyshev, 7. Saratov, 8. Volgograd, 9. Nyzhne-Kama, 10. Votkinsk, 11. Kama (Perm).

nance of species indicative of oligosaprobic and ß mesosaprobic conditions to those characteristic of OE and ß mesosaprobic conditions (Okhapkin 1978).

Phytoplankton primary production and biomass vary widely from year to year and in different areas of the basin, ranging between 0.10 and 2.25 g C• m^{-2}• d^{-1} (Romanenko 1978).

Data by Romanenko (1984) on the energetics of the Volga demonstrated that the ratio of primary production per m^2 to primary production per litre is a constant equal to 2 100. Extrapolating from this ratio and from long term survey data gives estimates of primary production of 31–168 g C• m^{-2} during the summer months between 1955 and 1974. Annual phytoplankton production from all Volga reservoirs is 2 164 000 t C based on an average of 106 g C• m^{-2} during the period when navigation is possible. This period coincides nearly exactly with the peak season of photosynthesis.

The contribution to total production by near-shore higher vegetation is generally low and only in Ivan'kov reservoir does it approach a third of the total input. Annual total primary production including that of higher vegetation, but excluding production by periphytic organisms, is 2 213 000 t C. The total organic content of Volga water decreases downstream and only increases again in the Delta (Bylinkina and Trifonova 1978). These figures are about 10 mg C• L^{-1} in Rybinsk reservoir and 7.2 mg C• L^{-1} in Astrakhan with some excesses in waste water discharges. The organic carbon content increases to 7.7 mg• L^{-1} below Astrakhan. The annual discharge of organic matter at the Volgograd dam is about 2 300 000 t, about half of which is discharged in the winter months (Sidenko 1976).

Annual decomposition rates in the water column have been estimated at 3 767 000 t C. About 25 % of primary production is lost to bottom sediments for an annual total of about 4 300 000 t C. The difference between this and primary production indicates the great significance of allochthonous organic matter to the total carbon balance of the system. The quantitative estimates of major sources and types of allochthonous organic inputs are not available. Annual commercial fish catch, in terms of organic carbon,

TABLE 1. The general morphometric characteristics of the reservoirs in the Volga and Kama rivers.

Reservoir	Replacement rate	Volume: Total km^3	Volume: Useful km^3	Area: Water km^2	Area: Shallow waters km^2	Length km	Width max. km	Depth: ave. m	Depth: max. m	Distance from mouth	Year of filling and/or reconstruction
Upper Volga											
Verkhnevolzhsk	1.1	0.794	0.526	179	—	92	4.4	4.4	16.1	3 425	1943-47
Ivan'kov	9.0	1.120	0.813	327	156	120	8.0	3.4	19.0	2 970	1937
Uglitch	9.7	1.245	0.809	249	89	143	5.0	5.0	23.2	2 834	1940
Rybinsk	1.3	25.420	16.670	4 550	950	250[a]	56.0	5.6	30.4	2 723	1941-47
Middle Volga											
Gorkov	6.1	8.700	3.900	1 591	368	430	15.0	5.5	21.0	2 275	1955-57
Tchoboksar	—	13.850	5.700	2 270	—	321	16.0	6.1	20.0	1 954	Under construction
Kujbyshev	4.1	58.000	34.600	6 450	1 035	484	27.0	8.9	40.0	1 470	1955-57
Lower Volga											
Saratov	17.8	12.870	1.750	1 830	329	348	20.0	7.3	32.0	1 122	1967-68
Volgograd	7.5	31.500	8.250	3 120	565	546	17.0	10.1	41.1	576	1958-60
Kama											
Kama (Perm)	4.3	12.200	9.200	1 915	400	272	13.5	6.4	28.6	631[b]	1954-56
Votkins	5.7	9.360	3.700	1 120	159	365	9.0	8.4	28.0	266[b]	1962-64
Nyzhne-Kama		12.900	4.400	2 650	550	300	20.0	—	25.0		Under construction

[a] Distance from Uglitch to Sheksna dam; the distance from Uglitch to Rybinsk along the ship's way is 112 km.
[b] Distance from Naberozhnye Tchelny.

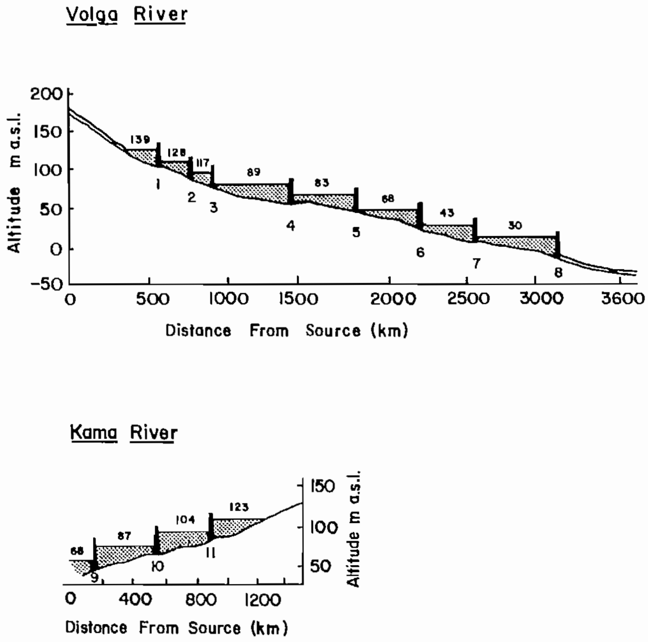

FIG. 2. Vertical profiles of the Volga River and its tributary, the Kama River. Numbers below dams denote the same dams and reservoirs as in Fig. 1, and the ones above reservoirs indicate meters a.s.l.

from the different reservoirs ranges from 0.033 to 0.077 % of primary production.

As catch estimates are within the limits of error of the estimates of primary production, it is evident that an evaluation of the status of the fishery based on energetic and ecosystemic data is not reliable. Furthermore, evaluations of other trophic levels (zooplankton and benthos) are not yet available.

The species composition of the predominant zooplankton changed significantly after the construction of the reservoirs, with Rotatoria being replaced by Crustacea. Certain Crustacea species (*Heterocope appendiculata*, *Eudiaptomus graciloides*, *Cyclops kolensis*, and others) whose distribution was previously limited to local areas of the riverine system are now common in a chain of reservoirs. The distribution of zooplankton is typically non-uniform in the reservoirs and the abundance decreases sharply in the river channel downstream of the dams only to rise again in the next lacustrine reach (Rivjer and Dzjuban 1978). The volume of planktonic outflow through the turbines is high; for instance 50 200 t of zooplankton were discharged from the Kujbyshev reservoir in 1975 and 35 000 t were discharged from the Saratov reservoir (Kuznetzova 1979). The discharge was almost entirely Crustacea, in accordance with a dominance of these organisms in reservoir plankton.

Benthic biomass varies with the age of the reservoir. Characteristically, colonies of *Dreissena polymorpha* tend to develop in suitable sites in the reservoirs throughout the system.

There appears to be no competition for food among fish species utilizing plankton or benthic food in reservoirs (Ivanova et al. 1978). This suggests that food availability does not limit fish production in the reservoirs. Thus a detailed study of energy flow is not necessary at present. We believe the survival of offspring is the major factor limiting fish production in reservoirs.

Hydrology

The long term annual discharge of the river at the level of Volgograd is 250 km^3 according to Voropaev and Velikhanov (1984). Fluctuation during the last 100 years ranged from a low of 161 km^3 in 1937 to a high of 383 km^3 in 1926. The present long-term discharge at Rybinsk dam is 1 020 $m^3 \cdot s^{-1}$ and at the Kujbyshev dam is

7 740 $m^3 \cdot s^{-1}$ (Fortunatov 1978). Sixty-five percent of the annual discharge passed in April–June before the construction of the cascade system, but subsequently this has changed significantly. The total area of the reservoirs is 26 000 km^2 and their storage volume is 88 km^3 (i.e. 35 % of discharge). In years with lower than average flows, the spring flood could be reduced by up to a half and during the dry season the discharge could be doubled. At present, 56 % of the discharge occurs during the dry season and 46 % during the high water period. In years of higher than average flows, this ratio would differ (Voropaev and Velikhanov 1984).

The Caspian Sea reached its lowest historical level in 1977 of about 29 m b.s.l., but has been increasing since then to 27.9 m b.s.l.

The Fish Community — Composition, Migration, and Distribution

Before human modification of the basin, 74 fish taxa and 2 species of Cyclostomata were found. At present, 88 taxa belonging to 18 families are present (Poddubnij 1978) (Table 2).

The increase in the number of taxa and their redistribution within the river are related mainly to the introduction of new species and their dispersion within the system. Of these, populations of *Ctenopharyngodon idella*, *Hypophthalmichthys molitrix*, *Aristichthys nobilis*, *Coregonus peled*, and *Anguilla anguilla* are sustained artificially. Other new species have entered the system through canals, including *Coregonus albula ladogensis*, *C. lavaretus lavaretus*, *C. lavaretus maraenoides*, *C. lavaretus nelmuska*, and *Stenodus leucichthys nelma*, which are all naturally reproducing. *Osmerus eperlanus* has moved southwards from the Beloye Lake and has penetrated as far downstream as the Kujbyshev reservoir. *Clupeonella delicatula* has moved northwards from the Delta (Kudersky 1970). The success of these species seems linked to the appearance of vast new pelagic habitats in reservoirs.

Some 30 taxa are distributed throughout the basin to form the permanent riverine assemblage. Some species within this assemblage also live within the North Caspian and enter the river to spawn or over-winter forming a second assemblage of semianadromous species (Table 3). A third assemblage of anadromous species also exists consisting of four species of Acipenseridae, three of Clupeidae and three of Salmonidae. These are: *Huso huso*, *Acipenser nudiventris*, *A. güldenstaedti*, *A. stellatus*, *Caspialosa brashnikovi*, *C. kessleri*, *C. caspia*, two forms of *Salmo trutta* (*S. trutta labrax* and *S. trutta caspius*) and *Stenodus leucichthys*. Many fish of this assemblage moved upstream for long distances before the construction of the dams which now obstruct their passage. For example, *Huso huso*, *Acipenser güldenstaedti*, *Acipenser stellatus*, and *Stenodus leucichthys* penetrated the Upper Volga as far as Kalinigrad and the anadromous Clupeidae as far as Gorky in the Middle Volga. Flow regulation has shortened these migratory pathways which are now confined to below the Volgograd dam. A number of species may reach the Saratov reservoir through fish passes which circumvent the two lowest dams.

TABLE 2. List of species of fishes and Cyclostomata, number of taxa and their distribution along the basin (after Poddubnii 1978).

		Number of taxa			
Family	Upper Volga	Middle Volga	Lower Volga	Delta	Total taxa
Petromyzontidae	1	1	1	1	2
Acipenseridae	1	2	5	5	5
Clupeidae	0	1	5	10	10
Salmonidae	10	4	3	3	15
Thymallidae	1	0	0	0	1
Osmeridae	1	1	0	0	1
Esocidae	1	1	1	1	1
Cyprinidae	20	27	27	30	32
Cobitidae	4	3	3	3	4
Siluridae	1	1	1	1	1
Anguillidae	1	1	0	0	1
Gadidae	1	1	1	1	1
Gasterosteidae	0	0	1	1	1
Syngnathidae	0	1	2	1	2
Atherinidae	0	0	0	1	1
Percidae	4	4	4	4	4
Gobiidae	1	2	4	4	5
Cottidae	1	1	1	1	1
Total	48	51	59	67	88

TABLE 3. Riverine and semi-anadromous assemblages of fish species.

Species		Riverine	Semi-anadromous
Acipenser ruthenus	(Linne)	*	
Esox lucius	(Linne)	*	
Rutilus rutilus	(Linne)	*	
Rutilus rutilus Caspicus	(Jakowlew)	*	
Leuciscus leuciscus	(Linne)	*	
Leuciscus cephalus	(Linne)	*	
Leuciscus idus	(Linne)	*	
Phoxinus phoxinus	(Linne)	*	
Scardinius erythrophthalmus	(Linne)	*	*
Aspius aspius	(Linne)	*	
Leucaspius delineatus	(Heckel)	*	
Tinca tinca	(Linne)	*	
Chondrostoma nasus	(Linne)	*	
Gobio gobio	(Linne)	*	
Alburnus alburnus	(Linne)	*	
Blicca bjoerkna	(Linne)	*	*
Abramis ballerus orientalis	(Linne)	*	*
Abramis sapa	(Pallas)	*	
Abramis ballerus	(Linne)	*	
Pelecus cultratus	(Linne)	*	
Carassius carassius	(Linne)	*	
Carassius auratus gibelio	(Bloch)	*	
Cobitis taenia	(Linne)	*	
Misgurnus fossilis	(Linne)	*	
Silurus glanis	(Linne)	*	*
Lota lota	(Linne)	*	
Lucioperca lucioperca	(Linne)	*	*
Lucioperca volgensis	(Gmelin)	*	
Perca fluviatilis	(Linne)	*	
Acerina cernua	(Linna)	*	
Cottus gobio	(Linne)	*	

Populations of anadromous and semi-anadromous fishes are completely migratory, whereas in riverine fishes the proportion of the populations which is mobile differs according to species. Unfortunately, systematic study of the fish populations of the river only began after the Volga had been connected to other basins and after its transformation into a cascade of reservoirs. Thus present-day population structures may now reflect the modified state of the river rather than its original condition.

The distribution of bream populations in the river between Ivan'kov reservoir and Astrakhan city (about 3 000 river km) does not correspond to any detectable chemical or thermal gradient. Rather, genetic interactions of three separate stocks — the Verkhnevolzhskii, Sheksninskii, and Kamskii led to two assemblages of populations in the basin (Yakovlev and Izyumov 1982; Izyumov 1984). Of two known forms of roach in Rybinsk Reservoir, one is present as a series of stable local populations, the other form is migrant and represents a single population. Two assemblages of inshore roach populations exist in the Volga basin, one in the Upper and Middle Volga, and one in the Lower Volga (Kasjanov et al. 1982). In Rybinsk reservoir the nearshore assemblage belongs to the Upper and Middle Volga population. Further development of population research should allow the tracing of microevolutionary responses to isolation of basins within the river and to changes in flow regime.

Productivity

The Volga–Kama basin provides about half of the total inland water catch of the USSR and about 85 % of the world sturgeon catch. In recent years mean total production in the reservoirs has been about 500 $\mathrm{kg \cdot km^{-2}}$. After the reduction in flow, the area of floodplain waterbodies in the Delta decreased by more than a third. As a result, catches of large food fish decreased from 100 000 t in 1960 to 31 000 t in 1978 (Butorin and Monakov 1984).

In the river, present catches from reservoirs considerably exceed those from the corresponding river reaches before impoundment (Kudersky 1984). Analysis of data of fish catches in the Volga reservoirs from 1976 to 1980 (Shimanovskaya et al. 1983) shows that there is a high positive correlation between reservoir area (A) in $\mathrm{km^2}$ and catch (C) in $\mathrm{kg \cdot yr^{-1}}$ ($R = 0.91$, $P<0.01$), with a regression $C = 0.734A - 259$.

Regression drawn through the 0 intercept does not differ significantly from the above, and has a coefficient of 0.623. Thus the mean annual catch from Volga reservoirs can be considered as 6.2 $\mathrm{kg \cdot ha^{-1}}$. These figures are based on commercial catches and the addition of recreational fish catch would increase the mean yearly catch per area considerably, perhaps to twice the commercial value (Poddubnij et al. 1978).

Catches from the Lower Volga River channel below Volgograd dam ranged from 120 to 215 $\mathrm{t \cdot yr^{-1}}$ from 1976 to 1980 with a tendency for catches to increase. Catches from the Akhtuba River and the lakes of the Volga–Akhtuba floodplain also tended to rise from 82 to 580 $\mathrm{t \cdot yr^{-1}}$ over the same period (Shimanovskaya et al. 1983).

The distribution of catch per unit effort (Table 4), (where CPUE was defined as 100 kg of catch • 100 $\mathrm{netdays^{-1} \cdot}$ 1 000 $\mathrm{ha^{-1}}$), shows the considerable differences that exist between CPUEs in the various reservoirs (Issaev and Karpova 1980).

TABLE 4. Catch per unit fishery effort.[a]

Reservoirs	1964	1968	1973	1978
Ivan'kov	4.6	2.8	3.8	3.3
Rybinsk	2.7	2.2	1.8	2.3
Gorkov	2.5	1.5	1.7	1.3
Kujbyshev	2.4	2.5	2.9	3.7
Volgograd	1.2	1.5	1.4	1.5

[a] 1 CPUE = 100 kg/100 net-days/1000 ha.

Management

Various management practices have been applied to the Volga River for the mitigation and rehabilitation of its fisheries.

Stocking

Fish farms have been built specifically for stocking the river to compensate for losses arising from environmental changes. About 90 000 000 young Acipenseridae and 18 000 000 *Stenodus leucichthys* are stocked annually to replace individuals which failed to be produced because of migratory difficulties. Thirty-six million farm-reared food fishes including bream, sander and carp are also raised (Nikonorov 1984).

Fish Passes

Three fish passes have been built, one each in the Volgograd and Saratov dams and one in the water splitter (more information on water splitter below), to allow the passage of brood stock of anadromous species, including sturgeon, stellate sturgeon, beluga sturgeon, cisco and others, upriver to the spawning grounds. Some 300 000 – 1 300 000 fish (including 4 sturgeon species, white salmon, and cisco) pass through the Volgograd fish elevator, and from 79 000 to 3 880 000 fish pass through the Saratov fish elevator each year (Issaev and Karpova 1980).

Research carried out during the design and construction of the fish passes indicated that it was possible to manage the distribution of fishes in pools downstream of the dams. Such management is mainly aimed at attracting fish to the fish collectors. The most precise tool for this is manipulation of water velocity which can be controlled to exceed selectively the swimming speed of certain species. By directing flows across the main water discharge, migratory fish can be deflected to concentrate at the mouth of a fish pass. Pavlov (1979) demonstrated that the distribution of fish in the tail waters can be simulated in the laboratory by use of small fish in aquaria. The number of fish attracted increases with flow velocity provided that critical swimming speeds are not exceeded. The vertical configuration of the attracting flow must conform to the vertical distribution of the migrating fish. For instance, for bottom-living species, the attracting flow must be directed along the bottom of the channel and suitable reference points for the fish must be present. Special attention must be paid to the timing of attracting flows where, by using data in daily migration rhythms, a schedule can be established whereby discharge is only regulated during the daily maximum for fish migration. New fish passes constructed at the weirs of the Kuban' and Don rivers successfully allow the passage of 65 % of the sturgeon and cyprinid species approaching the dam (Nikonorov 1984). In the Delta, deepening of distributaries and construction of 16 channels has allowed fish to enter the river from the sea.

Artificial Spawning Grounds

Several types of artificial spawning grounds have been tried and are being installed in the river. Artificial spawning "nets" simulate the submersed vegetation required for the breeding of phytophilous species and gravel deposits are laid down for the lithophils. Artificial spawning substrates prepared in collapsible ponds have been designed to test spawning performance of different species under various flow conditions in rivers, reservoirs, and tail races.

A unique reproductive complex has recently been finished in the Lower Volga which includes the water splitter. This complex, which serves to direct flood water between the east and west arms of the Delta, contains a fish pass and navigational lock. The eastern area of the Delta is the main spawning ground for semi-anadromous fish. A longitudinal earth dam situated between the deltaic areas prevents backflow across the floodplain. This structure has produced improved spawning grounds in the Delta which extend over 215 000 ha and its efficiency is indicated by an improvement in catch by 12 500 t since its installation (Nikonorov 1984).

Protection of Young Migrating Fish

Young fish tend to be sucked into water intakes of turbines during their downstream migrations. Eighty to ninety-five percent of such induction occurs during the night when fish lose visual orientation in the flow. Two main approaches have been adopted to prevent young fish from becoming entrained in this way (Pavlov and Pakhorukov 1983). Firstly, the ecological approach is based on a knowledge of the vertical and horizontal characteristics of the migration, both seasonally and diurnally. This then requires a spatial and temporal control of water use aimed at avoiding particularly unfavorable discharge patterns. Secondly, the behavioral approach relies on the responses of fish to different stimuli. Here the response of the fish to current and the correlation between flow velocity and speed of fish movements have to be taken into account (Pavlov 1979). For example, the sharper the angle of placement of a protective screen the more its efficiency rises with increasing flow. Screened structures are the most commonly used method for fish protection in the Volga system. Cone-shaped structures with fish deflectors are most effective for very strong water-intakes (3.5 $m^3 \cdot s^{-1}$). Water intakes of mobile pumping stations with low volumes ($<0.175\ m^3 \cdot s^{-1}$) are usually provided with a fish protection nozzle which deflects fish away from the intake.

Introductions

Several species of fish and fish-food organisms have been introduced into the Volga system. The most successful introduction has been *Nereis diversicolor* into the Caspian Sea. This worm is now the major component of the diet of sturgeons. Introduced fish species are listed under the heading "The Fish Community". Other invertebrate species which have been introduced successfully in Volga reservoirs are *Paramysis intermedia*, *P. lacustris* and *P. baeri* (Mysids), *Gmelinoides fasciatus* (an amphipod from Baikal Lake) and *Hypanis colorata* (a bivalvia mollusc).

Other Management Measures

Other measures for the management of fisheries of the Volga River include: control of pollution; improvement of water bodies; control of commercial and recreational fishing; protection of ichthyofauna during blasting for geological surveys and other activities. Eight nature reserves are located on the shores of the Volga. The oldest and largest reserve is the V.I. Lenin Astrakhan State Reserve established in 1919 in the Delta (USSR Natural Preserves 1980).

Three fishery research institutes and two biological institutes of the USSR Academy of Sciences work on the Volga fisheries. The protection of fish stocks and control of rational management are carried out by four Basin Departments of the General Department for the Regulation of Fisheries Fish Culture and Fishery Improvement (Glavrybvod).

The most significant success in the field of management of the Volga system is probably the preservation of commercially fishable stocks of sturgeon in the face of extreme ecological impact. The programme for rearing and release of young, the prohibition of the marine fishery and other measures have not only compensated for the decrease in natural reproduction due to damming, but have increased catches from 15 000 to 16 000 t in the 1960's to 24 000 to 27 000 t in the 1980's (Nikonorov 1984). Furthermore, the white salmon (*Stenodus stenodus*) has been restored. This species was included in the IUCN/UNEP Red Data Book and in the 1960's only 2 000 specimens were thought to exist. Population estimates from the early 1980's now put the abundance at 17 000 specimens (Nikonorov 1984).

Theoretical Aspects of Management — General Considerations

Sharp transformation in riverine ecosystems and in the composition and productivity of fish communities have resulted from human interventions in almost all large rivers of the world. This process can only be counteracted by management at the system level. Theoretically such management includes three ecological concepts: (i) protection of aquatic ecosystems and fish populations; (ii) careful management of the exploitation of stocks and of the aquatic resource; and (iii) planned construction of ecosystems. The extent to which any of these concepts or strategies can be applied depends on the aims of management, the particular conditions of the basin and the extent and nature of the impact.

Fish Migration and the Problem of its Control in Regulated Rivers

The outstanding feature of the Volga in common with many other large rivers is that its flow has been completely regulated and its channel converted into a cascade of reservoirs. Indeed, because of the control of flow the stretches of channel that remain unimpounded are also converted into reservoir type rivers. This change has restricted fish migration and distribution. This is of extreme importance to the management of fish stocks and, while admitting the significance of other approaches to productivity, we intend to concentrate on this particular aspect.

Fish migrations in inland waters generally conform to the three cycles presented in Fig. 3 which are defined not only by the temporal similarity of the migratory cycle, but by the spatial limits of the population range. Migratory cycles are characteristic not only of anadromous or semi-anadromous species, but are also found in purely freshwater fishes where the upstream spawning migration and downstream drift are common to all three behavioral types. The range of these displacements varies. The ratio of resident to transient individuals, as well as the degree of overlapping or the distance separating reproductive and trophic ranges differs according to fish species and may even vary in the same species under different conditions.

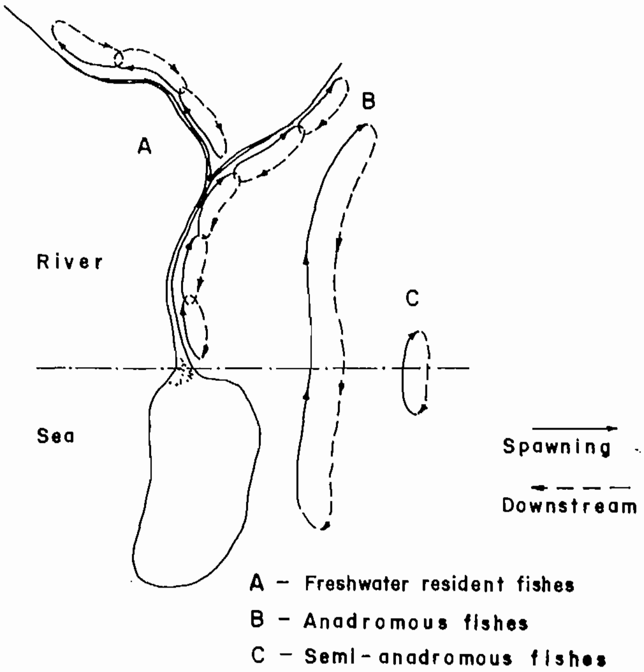

FIG. 3. Migration patterns of Volga River fishes.

As a result of hydro-technological activities, the migratory cycles are frequently broken. Upstream spawning migrations are interrupted by dams. Downstream migrations result in mortality of riverine species within reservoirs, the entrainment and death of fry in turbines and their transfer and isolation in irrigation channels. Dams of hydroelectric plants act as a kind of valve which permit downstream movement only, and are thus an important factor in the dynamics of the populations.

With regulation of river flow, sharp changes in the composition and abundance of fish populations may occur at three points in the system.

1) At the upstream end of the reservoir not all species drifting downstream find favorable conditions for survival and therefore die. For example, the slower rate of flow in the reservoir introduces discrepancies between the length of the migratory path and the timing of embryonic development. Eggs of pelagophil species therefore tend to sink and become covered with silt in the deposition zone at the upstream end of the reservoirs. On the other hand, the abundance of phytophil and eurybenthic fishes has risen sharply.
2) Within the reservoir many individuals are retained as they do not drift to the dam before they reach a size at which they are independent of the current through the reservoir.
3) At the outlet there is considerable mortality when fish are entrained in the turbines or the overspill because of differences in hydrostatic pressure. For example, in the Ili River, of the 19 species which drift through the Kaptchegeay reservoir, only one, the Zander, occurs below it (Pavlov et al. 1981).

Comparative investigations of drift in 22 different waterbodies, mostly from the Volga basin, (Pavlov et al. 1985), demonstrated that downstream migration of fish through waterbodies where current velocities are slowed, have certain features in common. The total length of the fish rarely exceeds 120 mm. Peak migratory activity occurs during the night, in accordance with the requirements of the fish for light to maintain visual orientation. Differences in species, size and number of downstream migrants, are related to flow conditions within the reservoir such as replacement rate (Total annual outflow from reservoir/Total volume of reservoir), the horizon from which water is removed and the form of the reservoir bottom. The success of downstream migration is thus related to the vertical distribution of the fish relative to the point of abstraction. In waterbodies with surface outflow, migrations occur mainly in the early months of the summer. In shallow waterbodies, most fish are transported downstream in the autumn as with the Cyprinidae. In reservoirs with outlets near the bottom, as in most Volga reservoirs, migration occurs all year round in species occupying the deep pelagial zone and is typical of Percidae, Osmeridae and Coregonidae. Seasonal variations in downstream transmission rates arise mainly because fish move towards the bottom as temperatures fall.

The major part of the population is lost in:

1) Pelagial species — smelt, pike-perch and cisco.
2) Sublittoral and benthic species — bream, bleak, perch, ruff.
3) Species inhabiting nearshore vegetated areas — pike, white bream, roach, ide, tench or rudd.

Pavlov et al. (1985) devised a migratory coefficient:

$K = (D/S) \times 100$

where D is the number of fish leaving the reservoir through drift per year and S is the abundance of species in the reservoir.

In Ivan'kov reservoir, fishes of the pelagial group had coefficients of 15–24 %. Attempts to increase production of the group in the reservoir by stocking failed due to the high migratory coefficient. In a second waterbody with a different flow structure (Seven Lake), whitefish, an introduced species, had a migratory coefficient of 0.46 % and formed the bulk of the fish catch.

Age composition, numerical abundance and seasonal dynamics of downstream migrants are all correlated with the water replacement regime of the reservoir. The degree to which these factors affect any particular species is determined by the overlap between the zone of influence of the outfall from the waterbody and the habitat of the fishes. Species present may also depend on the type of waterbody. Large planktivorous species are virtually absent from catches in reservoirs whereas they constitute up to 43.3 % of the total catch in large natural lakes in the same geographic zone (Kudersky 1974, 1984; Shimanovskaya et al. 1983).

Commercial pelagic species were abundant in catches only in Tzymlyansk (pike-perch, blue bream, sabre fish), Rybinsk (pike-perch, blue bream) and Verkhnevolzhsk (pike-perch) reservoirs where the replacement rate was lowest; 1.0, 1.3, and 2.6, respectively. Here downstream transmission of fish is lowest (Pavlov et al. 1981; Pavlov 1986). In contrast to lakes the pelagial zone of most reservoirs can only be populated by short-lived pelagic species because of their high replacement rates. Thus *Osmerus eperlanus* and *Clupeonella delicatula* are found in Europe and various species of small clupeids in African and North American reservoirs (*Limnothrissa, Cynothrissa, Pellonula*, and *Dorosoma*) whose population dynamics are well adapted to high mortality. Their reproduction is thus able to compensate for massive losses through downstream transportation.

The composition of fish communities in reservoirs depends on the migration conditions in the river–reservoir–river unit. Estimates of production anticipated from new reservoirs are often high because they fail to take into account the effects of downstream migration. The method of forecasting used in the 1950's assumed that productivity was similar in natural lakes and in artificial reservoirs. Catches from reservoirs were anticipated to be not less than those from natural lakes in the same climatic zone. The predicted and actual catches from the Volga reservoirs are compared in Fig. 4 (data from Kudersky 1974). Ivan'kov reservoir (dotted circles) was omitted from subsequent analysis because it differed from the others in physical form with large semi-isolated areas of shallow water. The correlation coefficient between replacement rate and the excess of predicted catch over the actual maximum catch (P) was $R = 0.829 : 0.01 < P < 0.005$, which shows a direct relationship between replacement rates and overestimates of catch in reservoirs. More detailed investigation revealed a tendency for fish biomass to decrease with increasing replacement rate particularly in pelagic species. Values for fish biomass were derived from Poddubnij's (1985) data for a number of reservoirs in the Volga and Kama rivers. The original data were obtained by echo-survey and experimental fishing of fish schools.

The scatter diagram in Fig. 5 plots the replacement rate (D) against the biomass of pelagic fish B (kg• ha^{-1}) for the Volga and Kama reservoirs with the omission of Ivan'kov reservoir. The fitted relationship:

$B = 27 + 63.6e^{-0.261\,D}$ ($r = -0.994$; $P<0.01$)

indicates that there is an exponential decrease in biomass as flow rate increases.

The nature of the relationship is significant in that it does not contradict the hypothesis that the reservoir ecosystem is an open-flow one. The turnover time of phyto— and zooplankton biomass is 1–2 orders of magnitude lower than the replacement time of the water in the waterbody concerned. Generally in non-regulated rivers replacement time of water in any given reach is less than the renewal period of the phytoplanktonic organisms, thus a true riverine plankton does not generally occur. Where flow is very slow and the growth rate of algal populations is high, blooms of laeustrine or near-shore forms occur. In lakes, the renewal period of the fish stock can be equal to or less than the replacement rate of the water. Thus a proportion of species with a low rate of renewal and a susceptibility to drift will be lost from the community. The abundance of other species would also depend on the replacement rate of the water within the waterbody concerned. The sensitivity of any fish species to overflow regimes depends on particular features of the out-

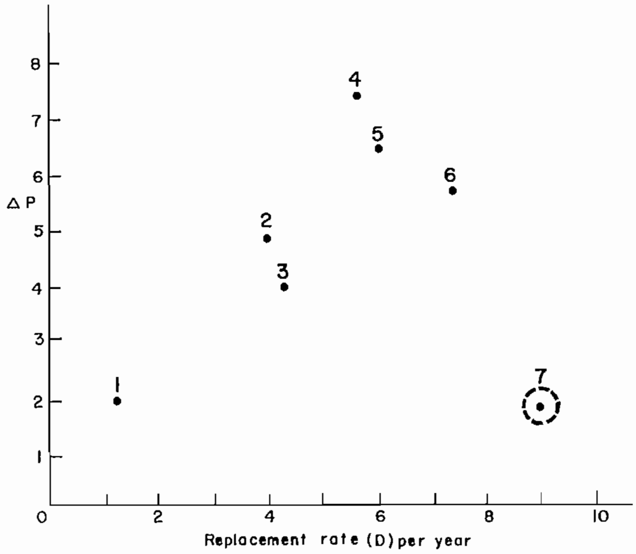

FIG. 4. Scatter diagram of predicted and actual catches from Volga reservoir. 1. Rybinsk, 2. Kujbyshev, 3. Kama (Perm), 4. Votkinsk, 5. Gorky, 6. Volgograd, 7. Ivan'kov.

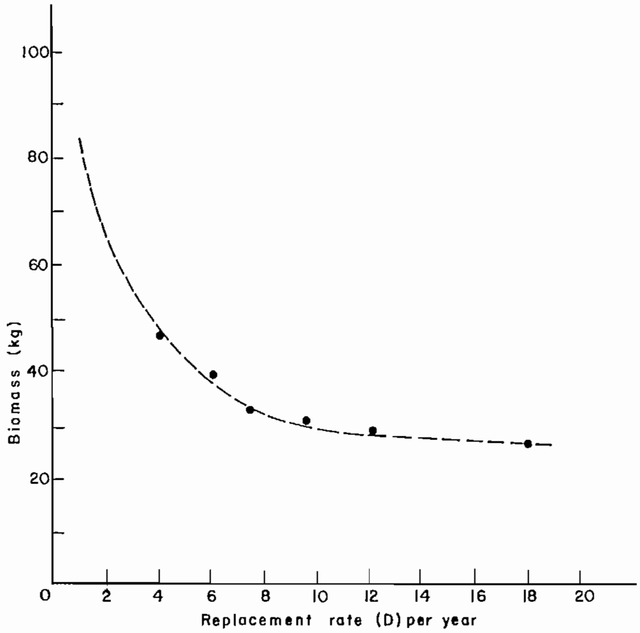

FIG. 5. Relationship between biomass of pelagic fish and replacement rate (D) for reservoirs of the Volga and Kama river systems.

fall, on the morphology of the waterbody and on the behaviour of the fish.

The high migratory capacity of pelagic species in the Volga resevoirs and the permanent loss of young fish during their passage through the turbines lead to the decline of the population and collapse of reproduction.

Several possible management strategies permit the reconstruction of migratory cycles under conditions of regulated flow.

1) Construction of fish passes: this is only obligatory in the case of anadromous and semi-anadromous species. In the case of fish permanently resident in freshwaters other strategies have to be applied.
2) Changing water renewal patterns from reservoir to lacustrine.
3) Prevention of fish drift by the use of fish protection devices.
4) Maintenance of the stock by release of young fish.

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References

Avakyan, A.B., and E.G. Romashov. 1970. Fishes conquer the dams. Mysl' Publ, (Moscow). (In Russian)

Butorin, N.V. 1978. *In* The Volga River and its life. Nauka Publ. Leningrade. p. 38–55.

Butorin, N.V., and A.V. Monakov. 1984. The contemporary ideas on biological resources and water quality in the Volga River and its reservoirs, p. 20–26. *In* The biological productivity and water quality in the Volga River and its resevoirs. Nauka Publ., Moscow. (In Russian)

Bylinkina, A.A., and V.A. Trifonova. 1978. Nutrient salts, p. 80–91. *In* The Volga River and its life. Nauka Publ., Leningrad. (In Russian)

Fortunatov, M.A. 1978. The physico-geographical characteristics of basin, p. 7–31. *In* The Volga River and its life. Nauka Publ., Leningrad. (In Russian)

1978a. The paleo-geography of drainage basin. *In* The Volga River and its life. Nauka Publ., Leningrad, p. 32–57. (In Russian)

Issaev, A.I., and E.I. Karpova. 1980. The fishery management of reservoirs. Pitshevaya Promyshlennost' Publ., Moscow. 304 p. (In Russian)

Ivanova, M.N., S.N. Polovkova, V.N. Kiyashko, and A.I. Bazhenow. 1978. The feeding and food relations of fishes in reservoirs of the Volga cascade, p. 55–77. *In* Theoretical aspects of fisheries investigations in reservoirs. Nauka Publ., Leningrad. (In Russian)

Izjumov, Yu.G. 1984. Population structure of the bream *Abramis brama* (L.) in the Volga reservoirs, p. 227–242. *In* Biological resources of reservoirs. Nauka Publ., Moscow. (In Russian)

Kasjanov, A.N., Yu. G. Izjumov, and V.N. Yakovlev. 1982. Morphological variability and intraspecific structure of roach *Rutilus rutilus* (Cypriniformes, Cyprinidae) in waterbodies of the Volga basin. Zool. Zh. 61 (12):1826–1836. (In Russian)

Kudersky, L.A. 1970. On the self-dispersion of some species of fishes. *In* Fisheries investigations of the inland waterbodies. Leningrad, Gosniorkh, No. 2. (In Russian)

1974. On the fishery resources in the reservoirs of the Volga-Kama river cascade. Izvestija Gosniorkh, v. 95. (In Russian)

1984. The present stage of fisheries utilization of reservoirs, p. 266–277. *In* N.V. Butorin and A.G. Poddubnij [ed.] The biological resources of reservoirs. Nauka Publ., Moscow. (In Russian)

Kuznetzova, V.I. 1979. The outflow of zooplankton from the Kujbyshevskoe and Saratovskoye reservoirs. Gidrobiol. Zh. 15 (1): 25–28. (In Russian)

Nikonorov, I.V. 1984. The 50th anniversary of Glavrybvod. Rybn. Khoz. (4):8–14.

Okhapkin, A.G.. 1978. The general characterization of saprogenic features of indicator species of phytoplankton, p. 140–144. *In* The Volga River and its life. Nauka Publ., Leningrad.

Pavlov, D.S. 1979. The biological bases of control of fish behaviour in the water flow. Nauka Publ., Moscow. 320 p. (In Russian)

1986. Migrations of fishes in inland waterbodies and their relation to flow. Zh. Obtsh. Biol. No. 2. (In Russian)

Pavlov, D.S., and A.M. Pakhorukov. 1983. The biological bases of fish protection against fish entering into the water intake devices. Ljogkaya i Pitshevaya Promyshlennost' Publ., Moscow. 264 p. (In Russian)

Pavlov, D.S., V.V. Kostin, V.K. Nezdolij, N.I. Gorshkov, and V.Yu Lobankov. 1985. The downstream migrations of fishes from the waterbodies with lowered water exchange. A.N. Severtzov Institute of Evolutionary Animal Morphology and Ecology of the USSR Academy of Sciences, Moscow. p. 137. (In Russian)

Pavlov, D.S., V.K. Nezdolij, R.P. Khodorevskaya, M.P. Ostrovskij, and I.K. Popova. 1981. The downstream migration of young fishes in the Volga and Ili rivers. Nauka Publ. Moscow. 320 p. (In Russian)

Poddubnij, A.G. 1978. Fauna of fishes, p. 228–247. *In* The Volga River and its life. Nauka Publ., Leningrad. (In Russian)

Poddubnij, A.G., V.M. Volodin, and A.N. Podlesnikov. 1978. The effect of recreational fishing on stock and composition of exploited fish populations, p. 143–150. *In* Theoretical aspects of fisheries investigations of reservoirs. Nauka Publ., Leningrad. (In Russian)

Poddubnij, A.G., K.I. Judanov, L.K. Malinin, A.S. Štrelnikov and I.I. Lapitzry. 1985. The density of fish stocks of the open inlets of the Volga reservoirs, p. 129–136. *In* L.S. Berdichevskij, T.F. Dement'eva, D.S. Pavlov and M.I. Shatunovskij [ed.] Theory of abundance forming and the rational management of commercial fishes (The Serial Edition "The Biological Resources of Hydrosphere and Their Use). Nauka Publ., Moscow. (In Russian)

Rivjer, I.K., and I.A. Dzjuban. 1978. The Zooplankton, p. 153–174. *In* The Volga River and its life. Nauka Publ., Leningrad. (In Russian)

Romanenko, V.I. 1978. The Microflora, p. 105–121. *In* The Volga River and its life. Nauka Publ., Leningrad. (In Russian)

1984. The primary production of organic matter in processes of photosynthesis in the cascade of Volga reservoirs, p. 48–59. *In* The biological productivity and water quality in the Volga River and its reservoirs. Nauka Publ., Moscow. (In Russian)

Shimanovskaya, L.N., T.V. Lesnikova, L.I. Tanasijtchuk, E.N. Shumakova, and M.I. Khalturina. 1983. The use of lakes, rivers and reservoirs of the USSR to fishery management, p. 3–92. *In* The fishery management in inland waterbodies and perspectives of its development. Collection of scientific papers. Leningrad, Promrybvod. (In Russian)

Sidenko, V.N. 1976. The hydrochemical regime of the Volgogradskoye reservoir in 1968–72, p. 3–16. *In* The Volgogradskoye reservoir. Saratov. (In Russian)

USSR Natural Preserves. 1980. A.M. Borodin and E.E.

Syrojetchkovskij [ed.]. Lesnaya Promyslennost' Publ., Moscow. 240 p. (In Russian)

VOROPAEV G.V., AND A.L. VELIKHANOV. 1984. The problems of water economic system of the Volga River, p. 6–19. *In* N.V. Butorin [ed.] The biological productivity and water quality in the Volga River and its reservoirs. Nauka Publ., Moscow. (In Russian)

YAKOVLEV, V.N., AND YU.G. IZJUMOV. 1982. The morphological variability and intraspecific structure of the bream of the Volga River, p. 171–193. *In* Ecology of aquatic organisms of Upper Volga reservoirs. Nauka Publ., Leningrad. (In Russian)

ZHADIN, V.I. 1950. The life in rivers, p. 113–256. *In* The life in Soviet fresh waters, Vol. III. Publ. of the USSR Academy of Sciences, Moscow-Leningrad. (In Russian)

Review of the Present State of Knowledge of Fish Stocks and Fisheries of African Rivers

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Abstract

WELCOMME, R. L. 1989. Review of the present state of knowledge of fish stocks and fisheries of African rivers, p. 515–532. *In* D. P. Dodge [ed.] Proceedings of the International Large River Sympodium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Africa has about 13 millions km of river channel of which some 680 000 are of stream order 5 or greater. Much of this length is concentrated in the basins of four main rivers but numerous smaller systems also exist. Several types of system are found on the continent, but the majority are tropical flood rivers. Biotic and abiotic factors in the rivers are conditioned primarily by the flood regime rather than by other climatic variables. The main source of nutrients and organic inputs to the aquatic system is allochthonous matter deposited in the lower order streams. Fish communities in African rivers are complex with numbers of species related to basin area. Fish habitats vary with flood state and many species are adapted to resist seasonally adverse conditions. Feeding, growth and mortality are seasonal, with reproduction in most species synchronised at the beginning of the flood, growth being limited to the period of rising water and mortality highest during the falling flood. Standing stocks and production are variable and are related to the area of water in the system. Fisheries are mainly artisanal and are also seasonal due to the difference in accessibility at various flood stages. Catch per unit effort is related to effort in a number of rivers by a power curve. Total catches tend to increase with increasing effort after which they reach a plateau which may be sustained over further increases in effort. This period of sustained yield is accompanied by shifts in the composition of the fish community. Catch in a river system can be related to main channel length, basin area or the maximum flooded area of the floodplain. Fisheries in African rivers are generally not managed effectively and change in water use patterns are liable to alter the nature of the rivers and their fisheries.

Résumé

WELCOMME, R. L. 1989. Review of the present state of knowledge of fish stocks and fisheries of African rivers, p. 515–532. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Les cours d'eaux de l'Afrique s'étendent sur environ 13 millions de kilomètres dont environ 680 000 appartiennent à la classe 5 ou à une classe supérieure. La plus grande partie de ces eaux sont concentrées dans les bassins versants de quatre grands cours d'eaux mais il existe aussi de nombreux petits systèmes. Le continent abrite plusieurs types de systèmes mais la majorité sont des cours d'eaux tropicaux à crue où les facteurs biotiques et abiotiques sont en grande partie déterminés par le régime des crues au lieu d'autres variables climatiques. Les matières allochtones déposées dans les cours d'eaux de classe inférieure sont la principale source de bioéléments et d'apports organiques dans le système aquatique. Les communautés piscicoles des cours d'eaux africains sont complexes, le nombre d'espèces étant lié à la superficie du bassin versant. Les habitats varient selon la situation des crues et de nombreuses espèces sont adaptées afin de résister à des conditions saisonnières défavorables. L'alimentation, la croissance et la mortalité sont fonction de la saison; ainsi, la reproduction chez la plupart des espèces a lieu au début de la crue, la croissance est limitée à la période de montée des eaux et le taux de mortalité est plus élevé au moment du retrait des eaux. Le stock actuel et la production varient et sont liés à la superficie des eaux du système. La pêche est en grande partie artisanale et saisonnière étant donné la variation de la facilité d'accès à différents stades de la crue. La relation entre les prises par unité d'effort et l'effort déployé dans un certain nombre de cours d'eaux peut être augmenter en fonction d'une augmentation de l'effort, après quoi elles atteignent un plateau qui peut se prolonger malgré une augmentation subséquente de l'effort. Cette période de rendement soutenu est accompagnée de variations de la composition de la communauté piscicole. Les prises dans un système fluvial peuvent être liées à la longueur du chenal principal, la superficie du bassin versant ou la superficie maximale inondée de la plaine d'inondation. En général, les pêches dans les cours d'eaux africains ne font pas l'objet d'une gestion efficace et toute modification du régime d'utilisation des eaux est susceptible de modifier la nature des cours d'eaux et des pêches.

Background

As a continent most of Africa remained sparsely populated and little developed until the second half of the twentieth century. Consequently, pressures on land and water over much of the continent were low and the environment was not stressed. Even today most African rivers have not changed significantly from their original condition and, although the land use in the surrounding basin may have been modified, the extent to which this has occurred is limited when compared with most other continental areas. Stresses on the rivers thus have remained low although one river, the Nile, supported one of man's earliest civilizations through the harnessing of the floods for irrigation. Large-scale abstraction of water for modern irrigation schemes has also been limited to a few rivers until now but the construction of large dams on most larger rivers in the 1960's and 1970's has had a considerable impact. Major reservoirs have been created behind such dams of which Lake Volta on the Volta, Lake Nasser on the Nile, Lake Kariba on the Zambezi and Lake Kainji on the Niger rivers are the largest. Other man-made stresses are relatively insignificant and although some cases of pollution, particularly with pesticides, have been reported, the scale and extent of pollution with toxic wastes and of eutrophication is still less than in any other continent.

The majority of African rivers lie in the intertropical zone, and of major streams, only the Orange River and the Deltaic reaches of the Nile have courses outside this area. This means that thermal regimes are generally relatively stable with a range from 20°C to 30°C and differ little from one river system to another. The main seasonal variable is rainfall allied to the typical intertropical succession of dry and rainy seasons. Several of the rivers lie within the sahelian zone and are thus exposed to periodic droughts during which the flow regimes are very much reduced. The main user of the African rivers and their resources has remained to date the fisherman.

Investigation of African rivers started on the Nile with the work of Wimpenny (1943) in Egypt and of Talling and Rzoska in the 1950's (e.g. Talling 1957; Rzoska and Talling 1966). At about the same time, a laboratory was set up on the Central Delta of the Niger (Blanc et al. 1955) whose output through the numerous publications of Daget clarified much of the taxonomy and biology of the fish of that river. Intensive but short-term studies were carried out on the Kafue river, which gave information on the dynamics and standing stocks of river fish (University of Idaho et al. 1971; University of Michigan et al. 1971). A team from the 'Organization de Recherche Scientifique et Technique d'Outre Mer' studied Lake Chad, the Chari River and the Yaeres floodplain of the Logone river during the 1970's. In addition to these major foci of river research in Africa, a large number of smaller individual projects have gathered information on many other systems and this review endeavours to collect and synthesize data on fish stocks and on fisheries drawn from these sources in order to propose a series of simple models for use in the development and management of such systems. This treatment is necessarily brief and more detailed information on the various aspects of African river fisheries can be found in Welcomme (1979 and 1985).

Morphometry

Types of Rivers

Classification of rivers is difficult but for fishery purposes in Africa, two categorizations are useful; (i) based on vegetation and (ii) based on flood regime.

(i) Rivers classified as to vegetation: Most African rivers flow through savanna or agriculturally modified landscapes. These range from wet savanna through dry sahel to semi-desert. A second group of rivers, situated mainly in equatorial Central and West Africa, are located in rainforest.

(ii) Rivers classified as to flood: Two main types of flood regime have been distinguished: flood rivers in which flow varies seasonally and reservoir rivers in which flow is distributed more or less evenly in time. Reservoir rivers are usually associated with rainforests or with some other geographical feature which stores water to release it slowly over long periods. They generally lack floodplains although they may be associated with extensive permanent swamps. Flood rivers are associated with floodplain systems of varying sizes.

Classification of the different reaches within the same river could follow that of Illies and Botosaneanu (1963) who divided rivers into a series of zones under the broad headings creon, rhithron and potomon. The last two of these categories refer to the upland rapids (rhithron) and the lowland, meandering and lenitic (potamon) river fascies.

Description of African Rivers (see Fig. 1)

The hydrography of the African continent is dominated by four major river basins, the Nile, the Zaire, the Niger, and the Zambezi. There are also numerous systems of secondary or tertiary importance, knowledge of which has contributed to the understanding of African river fisheries biology as a whole. Most African rivers remain relatively unmodified and are associated with extensive wetlands in the form of floodplains, swamps and lakes.

The Nile

The two main branches of the Nile rise separately as the Blue Nile in the mountainous terrain of Ethiopia and the White Nile in the highlands of Rwanda and the Lake Victoria basin. The White Nile expands into the Sudd of the Sudan which is located at the confluence of the Nile and the Bahr el Ghazal. Here the 16 300 km^2 permanent complex of papyrus swamp and openwater lagoon swells to twice this size during the river flood and additional areas of variable extent are flooded by rainfall and local runoff. A large waterway, the Jonglei canal, is currently being excavated to bypass the swamps and make more water available downstream. The Sudanese and Ethiopian Baro, Ghila and Akobo rivers also flood an extensive area of up to 6 000 km^2 which remains almost completely unsurveyed. The coastal delta of the Nile which provided the wealth of Pharaonic Egypt is now no longer inundated and the fringing floodplains of the lower course of the river virtually disappeared after the closure of the Aswan Dam. Although its origins are equatorial, the Nile flows for most of its 6 650-km course through savanna, sahel and desert.

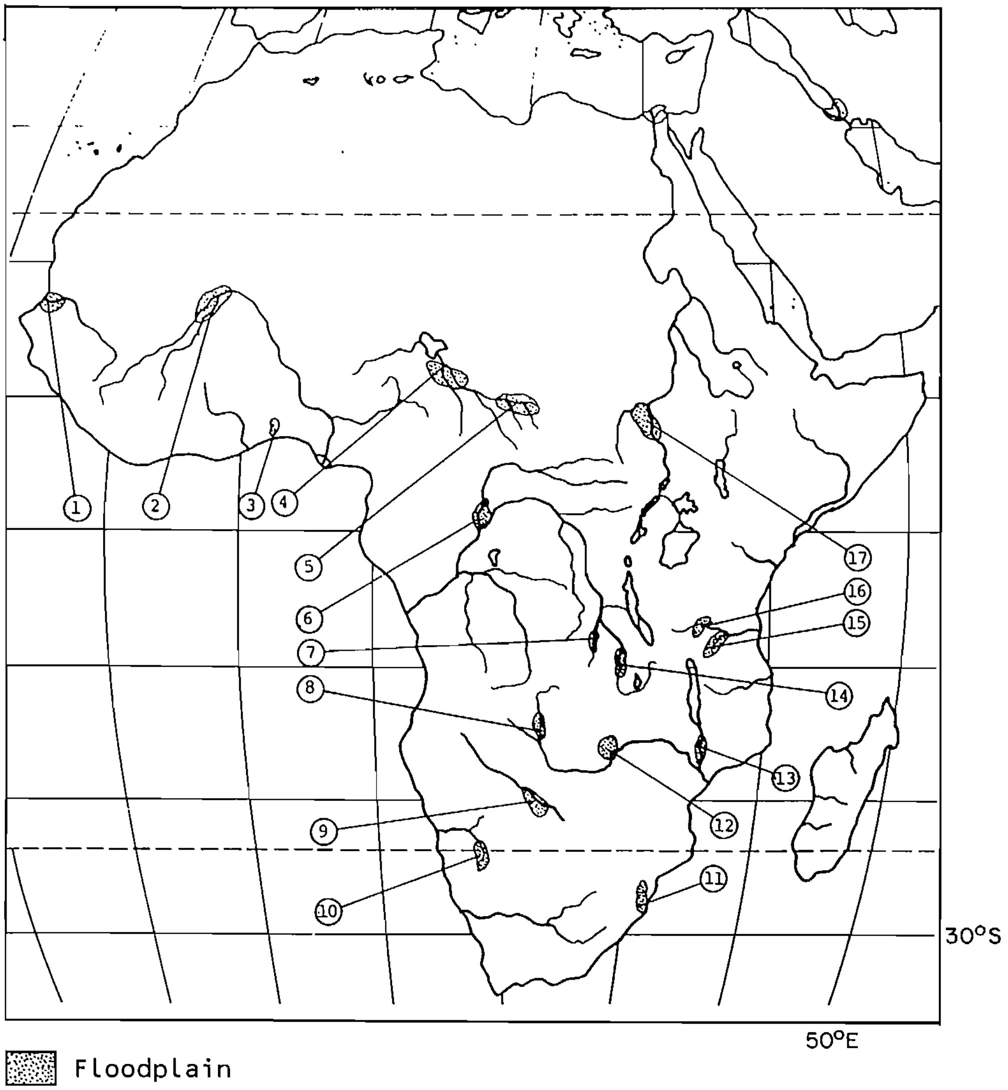

FIG. 1. Location of the major rivers and floodplains of Africa: 1. Senegal, 2. Niger, Central delta, 3. Oueme, 4. Logone, Yaeres, 5. Chari, 6. Zaire, Mbandaka, 7. Lualaba, 8. Barotse, 9. Okavango, 10. Cunene/Ovambo, 11. Pongolo, 12. Kafue, 13. Shire, 14. Luapula, 15. Rufigi, 16. Ruaha, 17. Nile, Sudd.

The Zaire

The 4 700 km main channel of the Zaire river arises in the high plateaux of Zambia and Zaire as the Lualaba and Luapula rivers associated with lakes Tanganyika and Mweru and the Bangweulu lake/swamp complex. It is joined by one major South flowing tributary, the Ubangui, and numerous North flowing rivers including the Lomani, Lomela, and Kasai systems. The tributaries generally rise in savanna zones to the North and South of the equator but their lower courses, together with the main course of the Zaire itself, lie within the equatorial rainforest. These geographic peculiarities impose two characteristics on the main system, firstly, a bimodal flood regime, and secondly, the nutrient poor acidic blackwaters characteristic of forest rivers.

The 3.97×10^6-km^2 Zaire basin is relatively poor in floodplains for its size. One 1 500 km^2 floodplain is formed by the Luapula river in the Kifakula depression between the Johnson Falls and Lake Mweru. Another occupies the Kamulondo depression where approximately 7 000 km^2 of permanent lake and swamp nearly double in area during the flood. A third flood area is formed below Kisangani where the river broadens to incorporate a vast complex of flooded forest at the confluence of the Zaire, Ubangi, and Sangha rivers.

The Niger

The Niger rises in the Fouta Djallon mountains of Guinea, flows in a loop passing first northwards through savanna then eastwards through the arid sahel, and finally southwards to pass through savanna and rainforest. It is joined in its lower course by its major tributary the Benue which rises in the Adamoua massif of Cameroon. Both rivers have fringing floodplains for most of their course. At peak floods, 5 981 km^2 of the Niger river plains in the Republics of Niger, Benin and Nigeria were inundated, although only about 35 % of this remained under water in the dry season. Much of the Nigerian portion of this plain has been lost since the closure of the Kainji dam. The Benue has a very impressive floodplain for its length with a flooded area of

3 100 km^2 and a residual area of 1 290 km^2 in Nigeria alone. The Niger has an extensive internal delta, produced where sand blown from the Sahara has deflected the channel near Timbuktu. A depositional plain has grown up behind this, with lakes lying in the depressions between rocky outcrops. It extends over 20 000 km^2 during the 4–5 mo flood, but its area shrinks to 4 000 km^2 in the dry season, most of which is retained in permanent lakes. The Niger has a coastal delta which covers 36 260 km^2, most of which is heavily forested, and also a coastal fringe of saline mangrove swamps.

The Zambezi

The origins of the Zambezi lie in the Central African uplands at the meeting of Angola, Zaire, and Zambia. The Upper Middle course of the river is flanked by the Barotse plains which flood laterally for up to 16 km from either bank. The combined area of the plains is over 10 000 km^2, although only 5 % of this area remains wet in the dry season. After passing over the Victoria Falls, which mark a transition between the Upper and Lower Zambezi fish faunas, and through the Kariba reservoir, the river is joined by the Kafue river whose waters are backed up by a range of hills to form the Kafue flats, over 6 600 km^2 of which are inundated during the rains. Only 1 465 km^2 of permanent waters remain throughout the year although the creation of a dam downstream of the flats has increased the extent and duration of the inundations. The Zambezi is later joined by the Shire river which rises in Lake Malawi. The Shire is noted for the Elephant and Ndinde marshes which cover 673 km^2 when flooded and shrink to 384 km^2 of swamp and lagoon in the dry season. These form part of a larger Shire river flood complex which has an inundated area of 1 400 km^2 and a residual area of 480 km^2. The Zambezi is 3 500 km in length and drains a total area of 1.28×10^6 km^2.

The Senegal

The 1 633 km long Senegal river arises in the Fouta Djallon and flows through arid terrain for most of its length. The river is flanked by a fringing floodplain which retains about 500 km^2 of water confined in slough lakes (66 km^2) as well as in the Lac de Guiers (150 km^2) and the main river channel (281 km^2). At peak floods the valley floor was covered to an area of 5 000 km^2, but damming of the river upstream has recently reduced this area substantially. The coastal delta of the Senegal has nearly 8 000 km^2 of annually flooded area.

The Chari

The Chari and its major tributary the Logone drain large areas of Central African savanna into Lake Chad. The floodplains of this system totalled about 90 000 km^2 in the 1960's of which about 70 % was inundated from September to October and only 7 % remain wet during April and May. Of this complex, the 7 000-km^2 Yaeres is the site of deltaic discharge of the Chari and Logone rivers into Lake Chad via the Logomatia and El Beid rivers. At least two other groups of floodplain are subject mainly to sheet flooding by rainfall and local runoff. The largest of these extends from the Bahr Aouk and Bahr Salamat over a considerable portion of Southeastern Chad and some 37 000 km^2 of Northwestern Central African Republic. The second group lies between the Chari and Logone rivers and spreads along the Bahr Erguig anabranch of the Chari.

Other Rivers

A large number of other rivers exist on the continent some of which have important features. For example, the Oueme river of Benin has a 1 000-km^2 coastal deltaic floodplain which terminates in a 180-km^2 brackish water lagoon. A large swamp complex is centered around the internal delta of the Okavango River and the 800-km^2 Lake Ngami. These swamps have a residual area of 3 120 km^2 and cover between 16 000 and 20 000 km^2 at high water. The Rufigi/Ruaha river system of Tanzania contains three large floodplains: the 1 451-km^2 fringing plain of the Rufigi river itself, the 4 400-km^2 Usungu plain of the Ruaha river, which includes the 518-km^2 Utungele swamp, and the 6 736-km^2 floodplain of the Kilombero tributary to the upper Rufigi, which contains the 89-km^2 Kibasira swamp. The Pongolo floodplain is small (130 km^2), but is of interest in that its upstream end is blocked by the Pongolapoort dam, which has permitted experiments on the discharge requirements for the maintenance of fisheries in small floodplains. An unusual type of flood wetland is formed by the overspill from the Cunene river in South Angola. In the wet season, this river discharges a considerable part of its flow southwards where it is contained within a graben. As it flows to the south through numerous channels and pools, the evaporation raises the salt content until finally the system becomes dry at the Etosha pan. Some 10 000 km^2 of this Ovambo floodplain consist of highly saline soils and water, but conditions are less saline towards the North where some 20 000 km^2 of waterways and floodable land are retained in a humid condition by ground water seepage.

Most African wetlands vary considerably in extent according to the medium term climatic regime. For instance, the Sahelian drought of the 1970's and 1980's reduced the area of the floodplains of the Niger, Senegal and Chari-Logone systems, whereas the increased pluviosity of the 1960's on the Central African plateau resulted in an enlarged Sudd. It is now suspected that the environmental impacts of such natural variations far outweigh the results of such human interventions as the Jonglei canal.

Statistical Parameters of African Rivers

Application of the statistical relationships between landform and various dimensions of rivers as defined in Leopold et al. (1964) shows the length of main river channels of African rivers to be related to basin area as follows:

$$L = 4.95\ A^{0.4521}$$

An approximate estimate of the number and length of river channels, ordered according to the Strahler (1957) system was carried out by Welcomme (1976) and yielded the following relationships:

$$\text{Number of stream} = 1.9719 \times 10^7\ (0.21^{\text{stream order}}), \text{ and}$$

$$\text{Stream length} = 0.695\ (2.3014^{\text{stream order}}).$$

TABLE 1. Estimated theoretical number and length of various orders of river channel in Africa (after Welcomme 1976).

Order	Number	Average length (km)	Theoretical total length (km)
1	4 166 969	1.6	6 667 150
2	870 615	3.7	3 203 865
3	181 900	8.5	1 540 693
4	38 005	19.5	741 097
5	7 940	44.8	356 347
6	1 659	103.3	171 358
7	347	237.4	82 492
8	72	547.1	39.392
9	15	1 259.1	19 013
10	3.2(3)	2.897.8	9 273
11	0.7(1)	6 669.0	4 668
Total			12 835 346

These relationships were combined to yield estimates of the total length of river channels of various orders as set out in Table 1.

Energy Flow

The energy flow of African rivers has not been studied to the same degree as rivers in some other tropical areas. It is to be supposed that, in common with other river systems, the most important input of nutrients to the aquatic system is through the influx of allochthonous material either falling directly into the system or washed in during the rains. A considerable amount of this material is eventually deposited on the floodplains where it may be recycled through consecutive flood and dry seasons. Additional nutrient and carbon inputs are obtained from the intensive use of the floodplain for agriculture and cattle grazing during the dry season, as wastes from these activities in the form of dung, and occasionally fertilizers, enrich the system.

Eisma (1982) pointed out that at 32 mg•L^{-1} the sediment load of the Zaire river was low when compared with tropical rivers from other continents. This also holds true for the Niger River with 78.3 mg•L^{-1} (Martins 1982) and the Orange river with 75.9 mg•L^{-1} (Hart 1983), but not for the Nile which has a load of about 1 400 mg•L^{-1} (Soliman 1983). Dissolved organic carbon (DOC) concentrations ranged from 2.0 to 6.5 mg•L^{-1} in the Niger R., from 3-5 mg•L^{-1} in the Nile R. (Soliman 1982), and from 2.0 to 2.8 mg•L^{-1} in the Orange river. In the Zaire River, mean values were about 8.5 mg•L^{-1}. Complex carbon molecules are present either dissolved in river water or absorbed onto fine particulate silt. These are usually in the form of sugars, mainly glucose, fructose, galactose, mannose, xylose, arabinose and rhamnose in African rivers, as observed for the Niger (Martins 1982) and Orange (Hart 1982); or amino acids and fatty acids as described by Visser (1970) and Balogun (1970). In the Niger, dissolved carbohydrate concentrations fluctuated seasonally around a mean of 0.36 mg•L^{-1} (min 0.1, max 1.6) and in the Orange River, concentrations ranged from 0.17 to 0.48 mg•L^{-1}.

Concentrations of inorganic nutrients, as indicated by conductivity, vary considerably among rivers, and even tributaries of the same river (Table 2).

TABLE 2. Conductivity and pH of some African river systems.[a]

River	Conductivity (k20 μmhos•cm^{-1})	Authority[b]
W. Africa		
Coastal		
Bandama	90-200	Welcomme 1972
Gt. Scarcies	60	Welcomme 1972
Konkoure	22.1	Livingston 1963
Lt. Scarcies	35-55	Welcomme 1972
Moa	36	Welcomme 1972
Oshun	57-96	Egborge 1971
Oueme	60	Welcomme, pers. obs.
Senegal	72	Reizer 1971
Niger system		
Upper Niger	31-70	Daget 1957
Lower Niger (Kainji L.)	46.6-99.6	
Mayo Kebbi	89	Leveque 1971
Volta system		
Black Volta	41-124	Welcomme 1972
Red Volta	62	Welcomme 1972
White Volta	119	Welcomme 1972
C. Africa		
Chari/Logone system		
Chari	22-73	Welcomme 1972
Logone	41-82	Welcomme 1972
Congo/Zaire system		
Zaire main stem	37.1-76.7	Gosse 1963
Ubangi	19.4-56.0	Micha 1973
Luapula	150-180	Soulsby 1959
Ruzizi	628	Marlier 1951
Lualaba	145-255	
E. Africa		
Ruaha	32-136	Petr 1974/76
Nile system		
White Nile	220-500	Hammerton 1972
Blue Nile	140-390	Hammerton 1972
Kagera	93-99	Talling and Talling 1965
Sobat	112	Talling 1957
Bugungu Stream	245-395	Welcomme 1969
Bahr-el/Ghazal (L.No)	550	Talling 1957
Semliki	400-910	Beauchamp 1956
S. Africa		
Orange	159	Keulder 1970
Zambezi system		
Kariba Lake	50-96	Coche 1968
Upper course (Barotse pl.)	57-126	FAO/UN 1969
Shire	220-450	Hastings 1972
Kafue	130-320	FAO/UN 1968
Lower course (Mozambique)	108-153	Hall et al. 1977

[a] These figures are often based on only a few observations and do not therefore necessarily reflect the full range of the parameters measures.

[b] Welcomme 1972 compiled data received in response to a circular FAO questionnaire.

The influence of nutrient concentrations on the productivity of the various rivers is not clear and no significant correlation between fish catch and conductivity was detected when these factors were analysed. Nevertheless, it is to be supposed that more detailed studies of primary productivity might show some relationship to exist.

Primary productivity in most African rivers is highly seasonal. The contribution made by phytoplankton is low except for occasional blooms in the main channel and floodplain water bodies during the dry season (Egborge 1974; Carey 1971). The majority of primary production is concentrated in higher plants, mostly trees on forested floodplains and grasses on savanna plains, although submersed vegetation also spreads rapidly in clear water areas. Few organisms appear to use higher plants directly in their diet and the entry of this material into the trophic chain depends on two main processes: the death and decay of dry season floodplain grasses during the floods, which produces a rich organic detritus, and the death, desiccation and decay of the wet phase grasslands during the dry season. Fire plays a particularly important role in accelerating the breakdown of organic matter during the earlier phases of the dry season and large areas of floodplain are burnt off by pastoralists to hasten the appearance of the dry season vegetation. Obviously, forest vegetation is recycled more slowly although slash and burn agriculture has accelerated the process in many tropical rainforest areas.

Zooplankton abundance follows a similar seasonality to that of phytoplankton (Holden and Green 1960; Monakov 1969), but plays a much more significant role in the nutrition of larval fish. Other important sources of food are the small plants and animals associated with the stems and root masses of submersed and floating vegetation as well as the abundant benthic organisms. Because of the large areas covered during the floods and the release of nutrients following inundation, there is an increase in the abundance and diversity of food items which contrasts with the general scarcity during the dry season.

Hydrology

The strongly seasonal nature of rainfall in the intertropical zone imposes an equally strong seasonal pattern on the hydrological regime of the rivers. At the tropics, precipitation is concentrated in a single season, from July to March in the Northern Hemisphere, and from November to March in the Southern Hemisphere. At the Equator there are two rainy seasons from March to May and August to November. The flood regimes reflect this timing with a single flood season in the second half of the year in northern rivers and in the first half of the year in southern rivers. Equatorial rivers have two flood periods per year roughly coincident with the floods in rivers to the north and south (Fig. 2).

Flood regimes of smaller order streams respond rapidly to local precipitation and are consequently 'flashy' in nature. As the area of the basin increases with stream order, the river receives rainfall from a larger and larger area and flood regimes become smoother. In extremely large basins whose tributaries arise in different climatic areas the merging of the different flood regimes may produce a second flood peak, as in the Niger River (see Fig. 3).

The accumulated precipitation generates a flood wave which is transmitted downstream at a velocity which is determined by the morphology of the basin. In the Niger R. the flood crest takes over 100 days to move 1 660 km from Koulikoro to Malanville, an average rate of travel of about 17 km•d^{-1} (Fig. 3). Similar speeds of transmission are found in the Senegal, where the 620 km from Galougo to Dagana take over a month (17 km•d^{-1}) and in the Chari, where the 745 km between Mossala and N'Djamena are traversed in 42 days (18 km•d^{-1} and in the Central Delta of the Niger, 13 km•d^{-1}, illustrating the principle that the more extensive the plain, the less its slope and the greater its vegetation cover, the slower the velocity of the flood wave. Because of the time taken for movement of the flood wave, its arrival at downstream sites may be delayed so that the floods do not coincide with the rainy season.

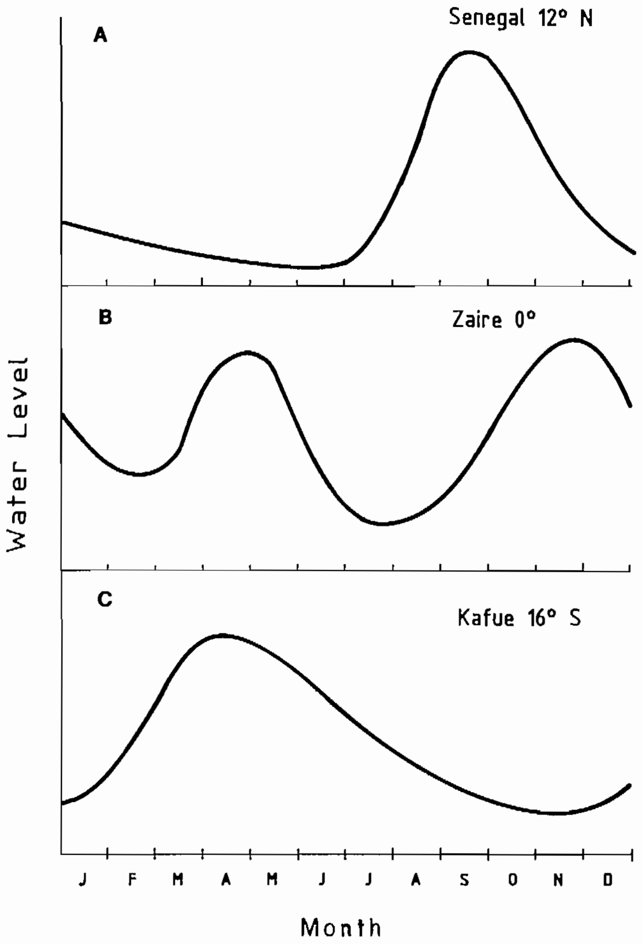

FIG. 2. Flood regimes of typical African rivers.
A. Senegal R. (12°N); B. Zaire R. (0°); C. Kafue R. (16°S).

Flow regimes in flood rivers are in a continuous state of change but three biologically active phases can be distinguished, rising water, falling water and low water. The flood occurs when rising water exceeds bankfull level to spill outward over the floodplain and lasts until the waters are once again contained in the main channel. The area inundated at peak flood, together with the amount (area) of water remaining in the system at low water, defines the severity and extent of the flood in any particular system. In African rivers, the ratio between area at peak flood and area at low water varies between a high value of 73 % and low values of 6–7 % (Table 3). Modal values are around 20 %, the mean

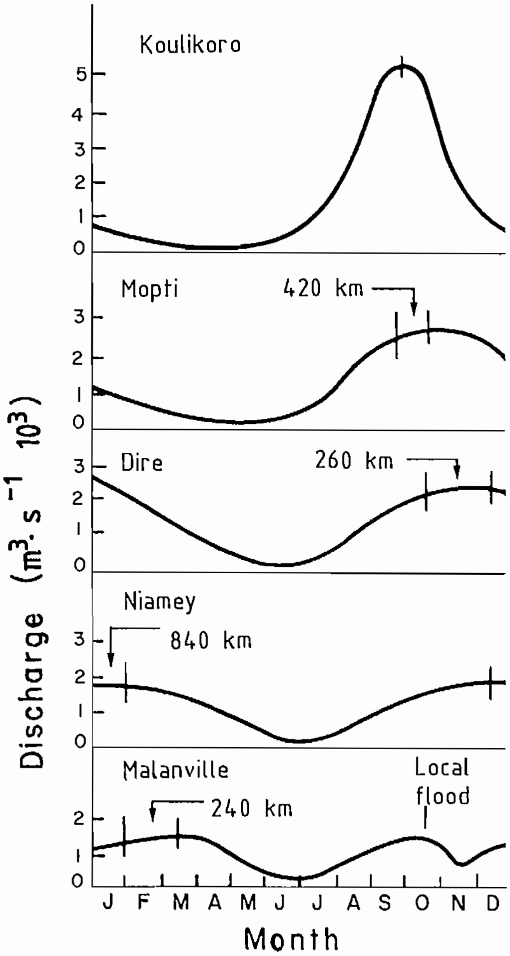

FIG. 3. Evolution of flood regimes in the Niger River.
The time taken by the flood wave to traverse the specified distance indicated by the vertical lines.

value is 29 ± 19%. Some floodplains with a particularly low percentage of water remaining in the dry season, such as the Oueme, have been extensively modified by agriculture which has filled many of the natural lagoons. Rivers with high ratios, have either extensive permanent lake systems on the floodplain as in the Shire R. and Kamulondo Depression, or have narrow fringing floodplains relative to the size of channel, as in the relatively low order Ogun and Oshun rivers.

Fish Community

Number and Size of Species in River Systems

The number of fish species found in the various rivers of Africa is closely related to basin area. The regression:

$$N = 0.44A^{0.434} \quad (r = 0.91)$$

describes the data for the 25 rivers plotted in Fig. 4. Actual numbers range from over 600 species in the Zaire to 12 species in the Me R.

The relationship between numbers of species and basin area for Africa is similar to that obtained for 11 river systems in South America:

TABLE 3. Characteristics of some African floodplains.

Floodplain	Area at peak flood (km²) 'A'	Area at low water (km²) 'B'	B×100 / A	Authority
Senegal R.				
Mean for total system	5 490	800	15	OMVS
Niger R.				
Central delta	20 000	3 877	19	Raimondo 1975
Fringing plain (Niger)	907	270	30	FAO/UN 1971
Fringing plain (Benin)	274	32	12	FAO/UN 1970
Fringing plain (Nigeria)	4 800	1 800	38	FAO/UN 1970
Benue R.				
Fringing plain (Nigeria)	3 100	1 290	42	FAO/UN 1970
Oueme R.				
Coastal delta	1 000	52	5	Pers. obs.
Chari and Logone R.				
Yaeres	7 000	NI	—	Ali Garam, pers. comm.
Total system	63 000	6 300	10	Blache 1964
Zambezi R.				
Barotse	10 752	537	7	FAO 1969
Okavango				
Internal delta	17 000	3 120	20	Cross, pers. comm.
Pongolo R.				
Fringing plain	100	26	26	Coke and Pott 1970
Kafue R.				
Kafue flats	4 340	1 456	27	Gay, pers. comm.
Shire R.				
Elephant and Ndinde marshes	665	200	30	Hastings, pers. comm.
Total system	1 030	480	38	
Luapula R.				
Kifakula (lagoon)	1 984	195		
depression (river)	1 500	75	13	
Total		266		
Lualaba R.				
Kamulondo depression	11 840	7 040	59	
Nile R.				
Sudd	31 800	16 300	51	Mefit-Babtie 1984
Volta R.				
Fringing plain Ghana	8 532	1 022	12	Vanderpuye, pers. comm.
Ogun R.				
Fringing plain	43	25	59	Dada, pers. comm.
Oshun R.				
Fringing plain	37	20	73	Dada, pers. comm.
Masilli R.				
Fringing plain	15	2	13	Dada, pers. comm.

$$N = 0.169A^{0.552} \quad (r = 0.95),$$

but differs in slope and intercept from relationships obtained

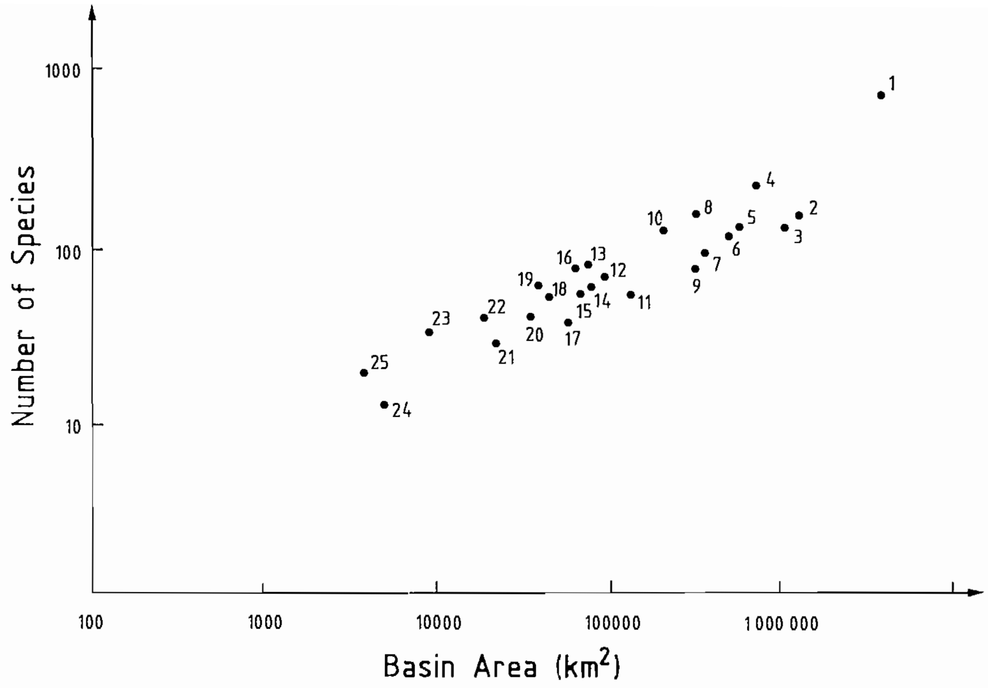

FIG. 4. Number of species recorded from various African rivers plotted according to basin area: 1. Zaire, 2. Zambezi, 3. Niger, 4. Ubangi, 5. Chari, 6. White Nile, 7. Volta, 8. Kasai, 9. Senegal, 10. Benue, 11. Cunene, 12. Bandama, 13. Gambia, 14. Sassandra, 15. Comoe, 16. Tana, 17. Ruaha, 18. Kafue, 19. Oueme, 20. Volga, 21. Cavally, 22. Shire, 23. Bia, 24. Boubo, 25.Me.

from more temperate areas (Daget and Economidis 1975; Eadie et al. 1986)

Species range in size from *Lates niloticus* which can reach a length of 180 cm and a weight of 160 kg, down to *Barbus lorenzi* with a standard length of 1.4 cm. Frequency distributions of length classes of species from African rivers show a predominance of small species. In the Niger, for instance, 50 % of species had a maximum length of less than 20 cm and 36 % a maximum length of less than 10 cm.

Distribution in Space and Migration

Distribution

The definition of ecosystems within flood rivers is difficult due to the constantly changing conditions following the fluctuations of the hydrological regime. There is effectively a constant, but repetitious, instability of habitat which corresponds to the 'pulse stable' systems of Odum (1967). Rzoska (1978) suggested that rivers can not be classified as ecosystems *sensus stricto*, a view to a certain extent echoed by the proposers of the river continuum concept (Vannote et al. 1980). The concept of habitat is similarly difficult to apply, as the same space within the system will be in a constant state of transition from one state to the next. Any definition of habitat must, therefore, contain a strong time component.

Most fish species occupy different habitats during the two seasons and may choose a third for reproduction. Thus each species is liable to have separate feeding, breeding and sheltering habitats and a corresponding pattern of migrations from one to the next. Some species spend their whole life within one type of habitat, either in the main channel of the river or in the permanent water bodies of the floodplain.

In rapids, a variety of species are confined to the main channel which are highly adapted to resist strong current by modifications of the mouth or fins into suckers or spines with which they cling to the bottom. Other species are adapted to life in the interstices of the rocks either by extremely small size or elongate body form. In the potamon too certain species, such as *Hydrocynus forskalli*, are confined to the river channels. The majority of species, however, are found in the main channels, or in any associated major lakes, only during the dry season when they take refuge from the generally adverse conditions pertaining elsewhere in the system.

Of the species that are normally confined to the floodplain, many have some physical or physiological adaptation to permit them to use oxygen from the atmosphere or from the surface layers of the water. Such species also segregate according to bottom type within the permanent water bodies during the dry season (Holden 1963) and move out of these onto the plain during the flood. During the flood, many additional species appear on the floodplain to breed and grow.

Migration and Movement

Movement between habitats may be classified into the following sequence although not all stages are followed by all species.

Movement of larvae to the juvenile nursery site
after hatching during rising water

**Fish generally spread over floodplain
throughout flood**

Movement of young-of-the-year and adult fish to
dry season refuge during falling water

**Fish generally confined in main river channel
or in permanent water bodies of the floodplain
throughout dry season**

Movement of maturing adult fish to spawning sites
on early rising water

Movement of adults to feeding sites on floodplain
during later rising water

Daget (1960) recognized two main components of such migrations: (a) longitudinal migrations in the main channel of the river, and (b) lateral migrations to and from the main channel over the floodplain.

Longitudinal migrations in African rivers rarely attain the proportions of the extensive movements of Asian or South American species. Nevertheless such migrations do occur. Potamodromous migrations from large lakes up inflowing rivers are common, having been recorded for instance from the Lake Chad system, where many species move up the Chari River to the Yaeres floodplain (Blache 1964: Carmouze et al. 1983); from the Lake Victoria–Nzoia River system, where 18 species were described by Whitehead (1969); and, for some mormyrids, characins and cyprinids of the Lake Mweru–Luapula River system (De Kimpe 1964). Some migrations take place over long distances. *Brycinus leuciscus* moved 400 km up the Niger from the Central Delta before the construction of the Markala dam at speeds of about 1–1.5 $km \cdot h^{-1}$ or 9 $km \cdot d^{-1}$ (Daget 1952). Fishermen from the Niger also say that similar distances are travelled by fish from the middle reaches of the river to the Central Delta. *Alestes baremoze* and *A. dentex* migrated for some 650 km from L. Chad up the Chari River (Blache and Miton 1962), and Williams (1971) recorded movements of up to 120 km in the Kafue River. In general, such migrations have been poorly recorded and studied in Africa, although it might be argued that the lack of traditional knowledge of widespread movements confirms that they are a relatively limited and local phenomenon.

Some information does exist on lateral movements, particularly on the return migrations of adults and juveniles from the floodplains on the falling flood. Observations by Durand (1970 and 1971) and Benech and Quensiere (1982, 1983 and 1984) showed that fish leaving the Yaeres floodplain for Lake Chad via the El Beid River did so in a fixed sequence largely determined by size and tolerance to low dissolved oxygen concentrations. Movements of fish onto the Niger River floodplains followed an inverse sequence with swamp tolerant species arriving earliest (FAO/Un 1970).

Feeding

Trophic Habits

There are relatively few detailed studies on feeding by fish in African rivers but those that do exist indicate the generally unspecialized trophic habits of most species. Specialists do exist, mostly piscivorous predators or such highly adapted forms as the tube snouted mormyridae which are able to exploit foods not readily available to other species. Many species are able to switch diets according to the relative abundance of food in the various hydrological phases. Typical examples are *Alestes* and *Brycinus* species which eat seeds, insects and some higher vegetation during the flood and phytoplankton at other times (Daget 1952), or *Alestes baremoze* which has a wide range of diet in various habitats (Paugy 1978). Even species with specializations aimed at one food source, for example the fine gill rakers of the planktonivorous *Heterotis niloticus* and *Citharinus* spp., utilize other food sources requiring the same adaptation, in thise case fine particulate muds.

Fine particulate muds and the organic molecules and bacteria associated with them are an important food source in the main channel and permanent floodplain water bodies of the potamon. For example, in the Lower Niger, Bakare (1970) showed that six of the most abundant species (*Citharinus citharus*, *C. latus*, *C. distichodoides*, *Labeo senegalensis*, *L. coubie* and *Barbus occidentalis*) depend mainly on this food source and that it is an important component in the diet of others including *Heterotis niloticus* and several *Synodontis* species. The abundant decapod crustacean fauna of African rivers also feeds heavily on these fine muds.

Coarser detrital material is of great significance as the basis of the trophic pathways in two different zones of the river. In the headwaters, particularly those under forest cover, the rain of plant material into the stream channel is the single most significant source of nutrients in the system. Many species feed directly on this material or on the numerous invertebrates which it supports. Seasonal deposition of coarse plant detritus on the floodplain contributes to the superabundance of food in this family of habitats during the flood. Allochthonous animal material is equally important in both low order streams and on the floodplain as nearly all species will feed on particles falling into the water.

Because of the large number of species in African rivers and their trophic flexibility, it appears that competition for food resources is not a serious factor in determining the composition and abundance of African riverine fish communities in the potamon. This is probably due to the excess of food that becomes available during the floods and to the general fast that fish undergo during the relative famine of the dry season.

The evidence available suggests that, although a wide range of food types are exploited, the succession of main trophic associations along an African river is the same as that found by Lowe-McConnell (1975) for tropical rivers in general. Fish in low order streams depend mostly on allochthonous food and there are few piscivorous predators. As stream order increases, generalized predators feeding on benthic invertebrates become more common and support an increased number of piscivores. In the lower reaches, the accumulation of detritus on the floodplains and soft muds in the permanent waters, favours detritivore or mud-eating forms and a very large population of piscivores preys upon them.

Seasonality

Feeding intensity is highly seasonal in African flood rivers and seasonality is found even in more stable riverine and lacustrine systems. There is generally a period of intensive feeding during the rising flood which diminishes as the waters begin to return to the river and ceases completely at low water. This coincides with the boom in primary and secondary production as water begins to spill onto the plain. There is some flexibility within this general time table with predators tending to reach peak feeding intensity as young-of-the-year are concentrating into the channels on falling water. However, even predatorial activity virtually ceases at low water in most species. Other species, particularly those specializing in allochthonous matter, mud or piscivorous predation, continue feeding well into the dry season (Willoughby and Tweddle 1978); Daget 1957) although even in these, general shortage of food may induce a fast as the aquatic system is further reduced in extent.

Intensive feeding during the floods permits fish to lay down stores of fat to carry them over the dry season and to elaborate gonadial tissue in preparation for breeding during the next flood. The build-up of fat during the flood, and loss of body weight during the dry season, result in fluctuations in condition factor with a maximum at bankfull on the falling flood and a minimum just before the next flood.

Growth

Seasonality of Growth

The strong seasonality of feeding by fish in flood rivers imposes a similar periodicity in growth which is reflected by rings on scales and other hard parts. Growth arrests have been distinguished from the scales of carnivores, herbivores, limnivores, insectivores and plankton-eating species in the Niger (Daget 1957), indicating the general nature of this phenomenon. The growth rate during the floods is such that Dudley (1972) found that 75 % of the expected first years growth of *Oreochromis andersoni* and *O. macrochir* took place within 6 wk prior to peak flooding in the Kafue Riverl. Growth during the first year of life is also particularly rapid. De Merona (1983), in studying the growth of over 100 African fish species, found little difference in the length of fish at the end of the first year of life from species having a wide range of maximum size. This may be a mechanism to avoid predation, as suggested by Lowe-McConnell (1967), but fish probably also need to reach an adequate size for migration by the time the floods recede.

The extent of growth in any one year appears to be related to the intensity and duration of the flood. Differences in growth related to year-to-year fluctuations in flood strength have been recorded in a number of fish species. For example Reizer (1974) detected great differences in growth of *Citharinus citharus* from the Senegal River in 1968, a year of particularly poor flood. Dansoko et al. (1976) showed the same effect for the floodplain spawning *Hydrocynus brevis* of the Niger River whose growth was poor in the drought years of 1971 and 1972. *Hydrocynus forskalii* which breeds in the river did not show this effect to the same degree. Significant correlations between growth and various measures of flood intensity were found by Dudley (1972 and 1974) and Kapetsky (1972) for several tilapias of the Kafue River and by Benech and Quensiere (1984) for species of the El Beid distributary of the Yaeres floodplain. Both Reizer (1974) and Dansoko et al. (1976) also found that species with poor first year growth continue to grow badly despite better conditions in later years to the extent that they can be overtaken by later year-classes.

Models of Growth

Most fish species from tropical rivers conform well to the Von Bertalanffy model in so far as their total yearly growth over their life is concerned. However this model does not describe adequately the more irregular within-the-year growth which is important for computation of production and for simulations. Daget and Ecoutin (1976) proposed a modification of the Von Bertalanffy model based on the growth of *Polypterus senegalus* from the Middle Niger. This model:

$$L_t = L_{max} \{1\text{-exp } [\text{-}g' \ (t\text{-}t_0)]\}$$

involves the addition to the original equation of two terms, q — which represents the duration of the annual growth arrest in months, and t — which is the duration of the first growth period in months; $g' = g/12\text{-}q$ and

$$t_0 = t_1 + \frac{\log(L - L_t) - \log L}{g' \log e}$$

The arc of the growth curve is thus compressed into 12 — q months followed by a horizontal line equivalent to q months. Kapetsky (1974[a]) proposed that the best description of growth by weight for the Kafue river tilapias was to rotate the relationship $W_t = W_o e^{gt}$ on its diagonal and reverse it to give an equation:

$$W_t = w_o + w_o e^{g(12)} - W_o e^{g(12\text{-}t)}$$

Reproduction

Fish inhabiting African rivers show a great variety of reproductive habits which permit them to cope with the particular difficulties of breeding in high flow, rapidly fluctuating water level and often extreme physical and chemical conditions. Physical and behavioural adaptations for reproduction seem more varied than those for feeding in these systems. As well as avoidance of adverse conditions, most breeding strategies succeed in placing the eggs on the floodplain at the beginning of the flood so that the larval and juvenile fish can spend the maximum period of time in this food rich environment whilst at the same time enjoying the protection that low population densities and high structural diversity afford. There is therefore a high degree of synchronization in the onset of breeding. One shot spawners almost all breed early in the rising flood and frequently undertake longitudinal migrations in the main river channel from the dry season refuge, as in the *Alestes* of the Logone River, which scatter large quantities of eggs in the channels leading into the Yaeres floodplain, or in the *Labeo* species which lay their sticky eggs on newly submerged vegetation. Other species move little from the oxygen poor habitats of the floodplain and show some form of parental care, for example, nest building in *Protopterus, Gymnarchus, Hepsetus* and *Heterotis*, mouthbrooding among cichlid species, and livebearing in *Pantodon buchholzi*. In most cases, these have lower egg productions per spawning than migrant species, but may breed several times in one flood season.

The intensity of the flood in any particular year can influence breeding success and the survival of fry. Riverine fish communities often show great variations in the relative abundance of species from one year to another. Failures of whole year classes due to poor flooding have been noted by Holden (1963) from the Sokoto, Reizer (1974) for *Citharinus citharus* from the Senegal and Carmouze et al. (1983) from the Chari. Furthermore, the contrast between the floodplain spawning *Hydrocynus brevis* and the channel spawning *H. forskalii* clearly shows that while poor floods diminish recruitment of floodplain spawners, channel spawners are less affected (Dansoko et la. 1976).

Mortality

In flood systems the distinction between density-dependant and density-independant mortalities becomes difficult as the two groups of factors are interrelated through the effects of the flood cycle. The two main causes of mortality in flood rivers are stranding mortalities during drawdown when fish are trapped in water bodies that either become deoxygenated or dry out completely, or predation which reaches a peak at the same time. Although there have been no studies on the mortality of fish during the flood period, it may be assumed that, with the great amount of food, lack of competition, shelter from predators and low densities, mortality is minimal during the flood but rises sharply as fish become more concentrated as water withdraws from the floodplain. Both causes of mortality persist through the dry season when numbers diminish steadily from predation and from the increasingly unfavourable aquatic environment.

This pattern of mortality contrasts with that predicted by the simple exponential model of mortality:

$$N_t = N_0 e^{-zt}$$

used to describe year-to-year mortality in fishes. In studying mortality of several species in the Kafue River, Kapetsky (1974[a]) proposed the model:

$$N_t = N_0 e^{-zt} (e^{zt} - 1)$$

where z is a weekly mortality coefficient, t = time in weeks and T = 52 weeks. Such a curve gives a mortality rate which increases steadily throughout the year and, while useful as a generalization for productivity modelling, still does not fully describe the numerical response of the fish stock to the fluctuating water regime. To compensate for shortcomings of existing models, Welcomme and Hagborg (1977) proposed an alternative equation for mortality linked to the density of fish and the flood regime as part of a more general simulation of floodplain fish populations (Fig. 5).

Production and Standing Stock

Several estimates of standing stock have been made in African rivers, usually by sampling with rotenone or electric fishing.

Main Channel

Estimates of ichthyomass in low order streams are uncommon in Africa where most work has been concentrated on larger systems. Some work has been done, however, in streams in Zaire and Zambia. Malaisse (1976) found standing stocks of 1.3, 26.1, 31.7 kg•km^{-1} in successive downstream reaches of the Luanza River. The succession in the Kaloma river studied by Balon and Coche (1974) was not so smooth, as an upstream reach with a standing stock of 21 km•km^{-1} and a downstream reach with 91 km•km^{-1} were separated by a steep torrential stretch with only 7 kg•km^{-1}. In the potamon of the Kafue River, University of Michigan et al. (1971) found an ichthyomass of 204 kg•ha^{-1} at low water. During further studies on this river, Kapetsky (1974[a]) found that the five main species alone had ichthyomasses of 106.5 ± 29.21; 386.6 ± 63.9 and 576.7 ± 129.2 kg•ha^{-1} in three separate reaches. Loubens (1969, 1970) sampled a 360 m^2 pool in the main channel of the Chari River at low water to find 861 kg•ha^{-1}. In the Bandama River, Daget et al. (1973) found a standing stock of 125 kg•ha^{-1} in January which fell to 50 kg•ha^{-1} in May. A second series of samples showed a similar loss in ichthyomass from 257 kg•ha^{-1} in January to 113 kg•ha^{-1} in August.

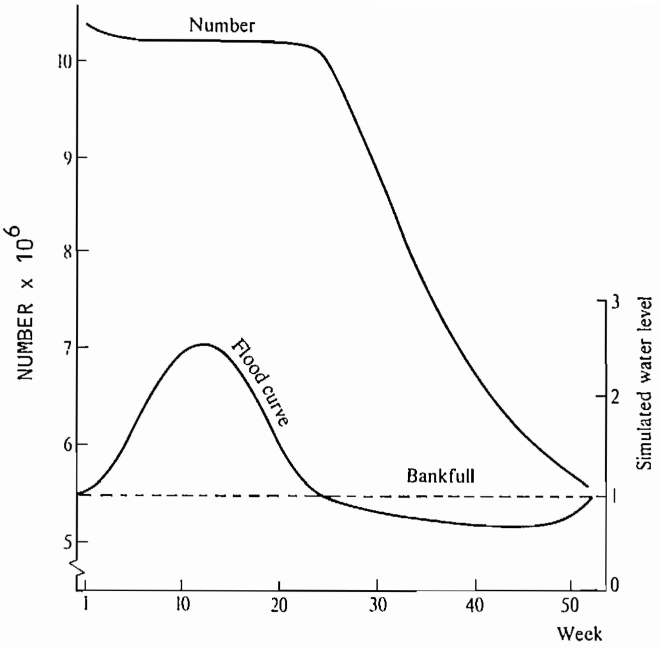

FIG. 5. Changes in the number of fish in one age-group over 52 wk as predicted by the simulation of Welcomme and Hagborg (1977). Also shown is the flood regime used in the simulation.

Backwaters

The degree of inter- and intra-year variability in the same water is indicated by samples from the Chari River where Loubens (1969, 1970) found 2 150 kg•ha^{-1} in one year; 5 616 kg•ha^{-1} at the beginning of the dry season of the next year, which dropped to 1 600 kg•ha^{-1} before the next flood, and 369 kg•ha^{-1} in a third year. Another backwater of the Chari had 2 150 kg•ha^{-1} in a 6 000 m^2 dead arm. One observation from the Bandama (Daget et al. 1973) showed a reversal of the more generally observed trend for the biomass of the fish to diminish over the dry season when 149 kg•ha^{-1} in March rose to 350 kg•ha^{-1} in June, this was probably due to immigration from the river to which the backwater remained connected.

Floodplain Pools

Samples of ichthyomass from standing waters of the floodplain also indicate extreme variability. This may be temporal, as in the Kafue, where one lagoon lost 75% of its ichthyomass in 6 months with populations falling from 2 693 kg•ha^{-1} to 684 kg•ha^{-1}. Another lagoon lost 85% of its population, from 3 306 kg•ha^{-1} to 501 kg•ha^{-1} in 10 wk (University of Michigan et al. 1971). There were also differences between wet and dry seasons; in the open waters of a lagoon in the dry season there were 426 kg•ha^{-1}, whereas in the floods there were 337 kg•ha^{-1}. Vegetated areas of the same lagoon showed the opposite tendency with very high concentrations of fish present under the vegetation during the floods (2 693 kg•ha^{-1}).

Other factors influencing populations may be the form of the lagoon, or bottom type. Reizer (1974) found 205 ± 155 kg•na^{-1} in round depression lakes and 13 ± 6 kg•ha^{-1} in elongated dead channels of the Senegal River floodplain. Holden (1963) found 1 012 kg•ha^{-1} over sand/mud, 785 kg•ha^{-1} over sand, and 233 kg•ha^{-1} over mud in floodplain pools of the Sokoto River. Nutrient status may also have an effect as standing stocks in the Okavango floodplain were far higher in lagoons enriches with cattle dung (700 kg•ha^{-1}) than in lagoons not so favoured (100–200 kg•ha^{-1}) (Fox 1976).

The high residual populations of floodplain pools during the dry season has been used by some fishing communities to create a type of extensive aquaculture. For example, the fishermen-farmers of the Oueme River in Benin cut numerous channel like ponds into the plain which serve as drains and also as reserves where airbreathing fish can survive until harvested at the end of the dry season. The mean yield of 34 drain-in ponds was measures at 2 099 kg•ha^{-1} in the 1950's and was still high at 1 571 kg•ha^{-1} for 34 ponds in the 1960's (Welcomme 1971).

Total System

Most sampling in African inland waters has been carried out by poisoning with rotenone. In small river channels the area to be sampled has been delimited by nets blocking the whole width of the channel (Malaisse 1969; Balon and Coche 1974), or by natural features such as rocky sills at the upper and lower end of the reach to be sampled (Daget et al. 1973; Loubens 1969, 1970). In the larger channels, lagoons and inundated floodplains of the Kafue, net enclosures were used by University of Michigan et al. (1971). Side arms of the main channel and small pools on the floodplain were poisoned in totality (Loubens 1969). In studying floodplain pools, other investigators relied on succesive fishings either to exhaustion (Holden 1963; Welcomme 1971; Reizer 1974), or as a basis for de Lury's method (Malaisse 1969).

The only estimate of the total standing stock of an African floodplain system so far attempted was that of University of Michigan et al. (1971) who extrapolated from a relatively sparse set of experimental data for the Kafue Flats to give 95 864 t (338 kg•ha^{-1}) in the flood and 57 405 t (435 kg•ha^{-1}) in the dry season.

The Kafue is also the only system for which estimates of biological production are available. Here Kapetsky (1974^{b}) found that *Tilapia rendalli* produced 198 kg•ha^{-1}•yr^{-1} of which 53% came from fish in their first year and 91% from fish in the first 2 years of life. Figures were similar for *Oreochromis andersoni* where 64% of the total 119 kg•ha^{-1}•yr^{-1} were produced in the first 2 years and *O. macrochir* where 74% of the 145 kg•ha^{-1}•yr^{-1} cam from this age-group. As these three species comprised between 53 and 73% of the standing stock, total annual production for the Kafue system may have been of the order 630–870 kg•ha^{-1}•yr^{-1}.

Comparison with Other Areas in the World

The figures obtained for standing stock and production of African rivers, and indeed from tropical rivers as a whole, compare well with those of temperate zones. There is as yet little evidence to support the supposition, derived from comparisons of series of lakes, that tropical waters are more productive than their temperate counterparts (Schlesinger and Regier 1982). In fact the range, mean and standard deviation of the standing stock from 17 tropical rivers [21.4 (154.4 ± 198.7) 861 kg•ha^{-1}•yr^{-1}] falls entirely within those of standing stocks for 26 temperate rivers [7.0 (205.0 ± 300.3) 1315 kg•ha^{-1}•yr^{-1}] described by a number of authors cited in (Welcomme 1985).

Dynamics of Floodplain Fish Communities

Despite the small amount of data from African rivers it is possible to draw certain conclusions as to the behaviour of fish communities under fluctuating hydrological regimes. It would appear that population densities are relatively low during the floods although the absolute population is high. As floods decline, population densities increase but the total biomass of the system begins to diminish. Later in the dry season, densities also diminish along with the total population.

Welcomme and Hagborg (1977) attempted a simulation to clarify these relationships based on the biotic parameters of a typical *Oreochromis* species. The curves derived from this simulation (Fig. 6) illustrate the constantly changing absolute and relative biomass, and consequently, the extreme difficulty is making comparisons either in the same or in different systems without knowing the precise stage of the flood when sampling occurred. Furthermore, the floodplain models for growth and mortality elaborated by Kapetsky (1974^{a}) and others give very different projections of production from the more normal simple exponential expressions. Floodplain models would predict higher production and greater surplus biomass, conclusions which have great importance for the management of river fish communities for fisheries.

The Fishery

Nature of the Fishery

African river fisheries are artisanal or subsistance in nature. Traditionally, they are pursued with a variety of gear, most of which is adapted to the capture of a limited range of species under particular conditions. More recently, fisheries have been based more on gill nets or cast nets made of modern nylon twine. Fishing is highly seasonal in all rivers and there is generally a regular succession of gears with a dominance of active methods in the dry season when fish are relatively static and passive methods when the fish

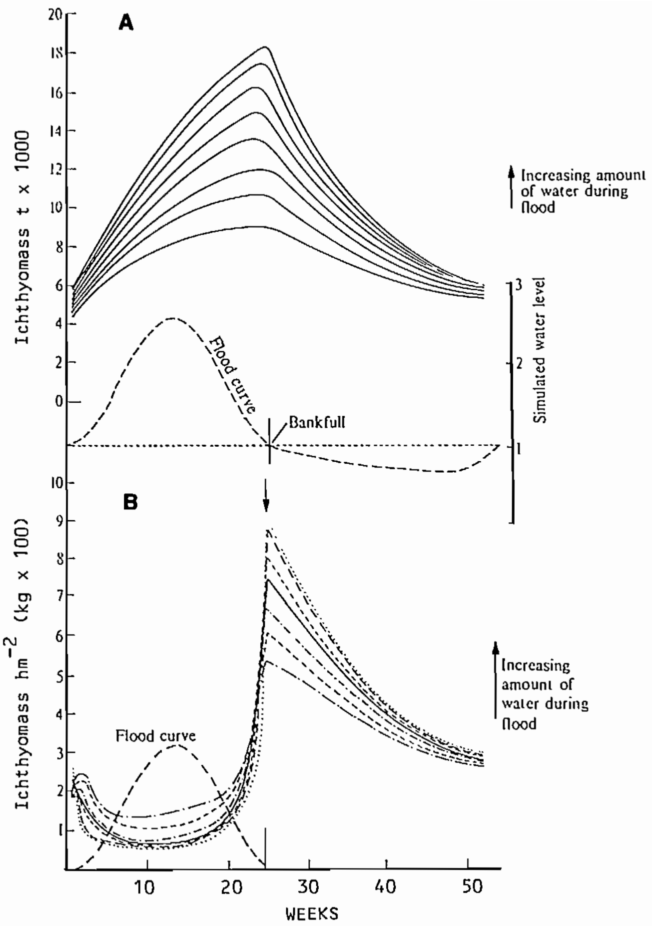

FIG. 6. Computer generated curves showing changes in (A) total ichthyomass and (B) population density with time for different flood regimes.

are migrating during rising and falling water (see Fig. 7 for example). Normally all fishing activity ceases during the floods when the fish are dispersed and physical conditions are unfavourable to the setting of gear.

Responses of Exploited Communities

Data from African river fisheries is sparse and generally of dubious reliability; however, some attempt at analysis is necessary to understand the ways in which exploited communities behave and to formulate management strategies based on this understanding. Two approaches may be adopted: firstly, the analysis of the history of fisheries in one river basin; and secondly, the comparison of data from a number of similar basins whose fisheries are at different developmental stages. In Africa, both approaches are possible as observations are available on the critical parameters of floodplain area, catch and number of fishermen, for several basins (Table 4). There is also a continuous data set from the Nile where Borhan (1981) has recorded the catch per boat over a 10-yr period.

Traditional stock assessment models have been applied rarely to African river fish. Durand (1978) studied the population dynamics of *Alestes baremoze* of the Lake Chad basin and Kapetsky (1974[a]) studied growth, mortality and production in several species of Kafue river fish. Such studies are overly demanding in time, funding and expertise for general application, and their use can also be questioned on more basic grounds. Traditional models may be applied successfully to individual species, but the behaviour of complex fish communities to fishing pressure is totally different from that of single stocks. Welcomme (1986) explored the various relationships governing fish yield in rivers in general.

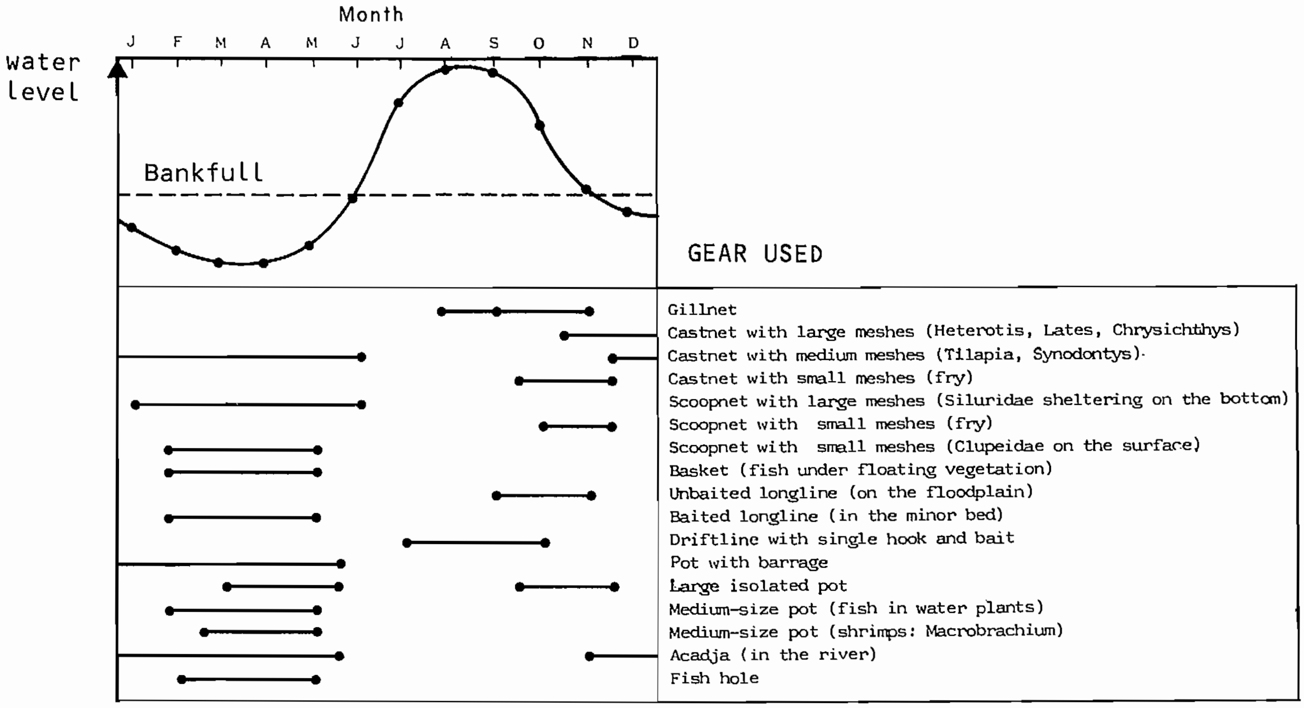

FIG. 7. Fish gear utilization in the Lower Oueme River during the course of 1 yr.

TABLE 4. Maximum flooded area, catch and number of fishermen for some African floodplains.

River	Area (km^2) 'A'	Catch (t) 'C'	Fishermen 'F'	CPUA ($kg•ha^{-1}$)	F/A	C/F
AFRICA						
Niger (Benin)	242.00	1200.00		49.59		
Niger (C.D. Mali)	20000.00	90000.00	54112.00	45.00	2.71	1.66
Niger (Niger 1965)	630.00	4700.00	1314.00	74.60	2.09	3.58
Niger (Niger 1982)	600.00	3200.00	3200.00	53.33	5.33	1.00
Niger (Nigeria)	4600.00	14340.00	4600.00	31.17	1.00	3.12
Benue	3100.00	9570.00	5140.00	30.87	1.66	1.86
Massilli	150.00	475.00		31.67		
Pongolo	104.00	400.00		38.46		
Shire (1970)	665.00	9545.00	2445.00	143.53	3.68	3.90
Shire (1975)	665.00	7890.00	3324.00	118.65	5.00	2.37
Yaeres	7000.00	17500.00		25.00		
Logomathia	600.00	300.00	70.00	5.00	.12	4.29
Kafue (1963)	4340.00	8554.00	1112.00	19.71	.26	7.69
Kafue (1970)	4340.00	6747.00	670.00	15.55	.15	10.07
Kafue (1982)	4754.00	7400.00		15.57		
Oueme (1957)	1000.00	10400.00	25000.00	104.00	25.00	.42
Oueme (1968)	1000.00	6500.00	29800.00	65.00	29.80	.22
Senegal	5490.00	30000.00	10400.00	54.64	1.89	2.88
Pendjari	40.00	140.00	65.00	35.00	1.62	2.15
Barotse	5120.00	3500.00	912.00	6.84	.18	3.84
Rufigi	1450.00	3589.00	3000.00	24.75	2.07	1.20
Kilombero	6700.00	14700.00	11260.00	21.94	1.68	1.31
Cross	8000.00	8000.00	4000.00	10.00	.50	2.00
Nile (Sudd)	31800.00	28000.00		8.81		
Nile (Egypt)	800.00	8410.00	3725.00	105.00	4.66	2.26
Kamulondo	6639.00	7355.00		11.08		

Catch Per Unit Effort Related to Effort

Evidence from a number of different rivers as well as that from the Nile fishery indicated that the relationship between effort and catch per unit effort (CPUE) is best described by an inverse power curve of the form:

$$CPUE = 11{,}117\ E^{-1.03}$$

for the Nile. Analysis of the group of rivers is more complex and, although the points conform to a relationship:

$$CPUE = 2.70\ E^{-0.48}$$

The scatter may also be interpreted as two distinct relationships:

$$CPUE = 2.58\ E^{-0.42}$$

for fisherman densities between 0.5 and 3.0 fishermen•km^{-2} and:

$$CPUE = 12.6\ E^{-1.14}$$

for densities of between 3 and 30 fishermen•km^{-2}, which better describe the distribution of points (Welcomme 1986).

Total Catch as Related to Effort

The form of the relationships of CPUE to catch predicts a rapid rise in total catch as effort is applied to the fishery followed by a phase where catch levels change little despite continued increases in effort. The Nile, for instance, produced 8 410 ± 542 t•yr^{-1} without any trend to increase or decrease over 10 yr despite a threefold increase in the number of boats operating on the river. The plateau phase of the exploitation curve masks a series of changes in the composition of the fish community. These changes involve the progressive elimination of the larger individuals and species from the fishery and their replacement by a sequence of smaller and more productive species (Welcomme 1986) in a manner to that described by Rapport et al. (1985) for other stressed ecosystems. There is a final phase in the exploitational history of a fishery when the effort exceeds the capacity of the fish community to compensate for the quantity of fish extracted. When this happens there is liable to be a growing instability in catch levels from year-to-year due to increasing dependency of the fishery on one year class of fish, followed by a fairly abrupt decline in catch. Complete collapse of river fish communities appears to be rare, although severe declines in catch based of fishing alone have as been recorded from the Oueme river (Republic of Benin).

Evaluation of Catch

Despite the poor quality of data from African river fisheries, Welcomme (1976) was able to derive relationships between catch and floodplain area, river basin area and main channel lenght, with surprisingly good correlation coefficients. These relationships have proved useful in general management for estimating fish production from rivers outside the original set, for establishing a global figure for inland fish production from Africa and for assessing the possible impacts of hydraulic works within river basins. Additional information has permitted a recalculation of the 1976 equations, but has not altered in any way the basic conclusions to which they lead.

Variations in Catch with Area of Floodplain

The assessment of catch in rivers is complicated by differences in fishing effort and in morphology between river systems. Morphological variation mostly lies in the presence, in some systems, of large floodplains or marshlands which form the basis for particularly intensive fisheries. In analysing the yield of African floodplains, Welcomme (1976) was obliged to distinguish between systems where the floodplain has an area greater than 2 % of the basin area from those with more normal development of the floodplain. A mean of 46.09 ± 37.62 $\mathrm{kg{\cdot}ha^{-1}}$ of flooded area is obtained from a sample of 26 African floodplains, but if fisheries with less than 1 $\mathrm{fisherman{\cdot}km^{-2}}$ of floodplain are excluded, the mean rises to 60.25 ± 36.53. The information available on the fisheries of other tropical river systems indicates that yields per unit area of savana rivers in Asia and South America do not differ significantly from those of Africa. Yields of some temperate systems, such as the Danube and the Mississippi, also fall within a similar range (from data compiled in Welcomme 1985).

Variation in Catch with Basin Area

The relationship between catch and river basin area for 20 rivers is:

$C = 0.3\,A^{0.97}$ (r=0.91)

where C = catch in tons and A = area in km^2.

Variations of Catch with Main Channel Length

The relationship between catch and main channel length is:

$C = 0.0032\,L^{1.98}$ (r=0.90)

from which may be derived estimators for catch from any reach of river. From these, the catch per kilometre of river increases from source to mouth according to the equation:

$C_k = 6.49k^{0.97}$

where C_k = catch in kg at river kilometre k.

Variations in Catch with Flood

The above relationships may be taken to represent a mean condition, but there is considerable year-to-year variation in catch within any one fishery. This arises from the biological consequences of differences in flood intensity between years. The better survival and growth of fish in years of good floods is transmitted to the fishery in the same or subsequent years. Relationships of the general form:

$$C_y = a + b(p\mathrm{HI}_{y-1} + p\mathrm{HI}_{y-2}\ \ldots\ldots\ldots\ldots\ldots\ p\mathrm{HI}_{y-n})$$

where HI = index of flood intensity and p = relative importance of a particular year, have been calculated for the Kafue, Shire, and Niger rivers (Welcomme 1979) as:

Kafue: $C_y = 2962 + 70.54(0.7\mathrm{HI}_{y-1} + 0.3\mathrm{HI}_{y-2})$
Shire: $C_y = 5857 + 38.11(0.9\mathrm{HI}_{y-1} + 0.1\mathrm{HI}_{y-2})$
Niger: $C_y = 3239 + 32.10(0.5\mathrm{HI}_{y-1} + 0.5\mathrm{HI}_{y-2})$

More recent information from the Kafue indicates that the overall trends in catch predicted for this river have continued despite the greater area flooded following the construction of dams at both ends of the Flats. In the Niger, further analysis of 20 yr of data (Welcomme 1986[a]) has indicated a shift in the proportionality of influence of the preceding years flooding with a regression:

$$C_y = 151.73 \log(0.7\ \mathrm{HI}_{y-1} + 0.3\ \mathrm{HI}_{y-2}) - 4281.26$$

The log-normal form of this relationship shows a lessening of response by the fish community to floods exceeding a certain level and a rapid increase of sensitivity as floods are reduced. This indicates the sensitivity of floodplain fishes to low water regime induced by human interference or, as in case of the sahelian rivers, by natural catastrophies.

Other authors have successfully attempted similar analyses in other rivers, noteably Krykhtin (1975) for the Amur, Holčík and Bastl (1976, 1977) for the Danube and Novoa (1982) for the Orinoco.

Management

Management of African inland waters has to be pursued within the framework of developing economies. This means that traditional management, sanctioned by local custom or religious belief, is still strong in many areas, and its replacement by more modern methods necessitates widespread modification of the whole socio-economic framework of the societies concerned. Management of fisheries in African river systems by governmental organizations is particularly difficult under these conditions and is still at a relatively early stage of development. Attempts at legislation for limitation of access, mesh-size restrictions, or closed seasons, have been made in some basins although the rationale for the limitations imposed is often arbitrary and enforcement is difficult. Furthermore the information base needed to formulate such policies is frequently lacking at a national level and interchange of data between states sharing a river basin is virtually non-existent.

The complexity of the problems facing management of tropical river fisheries has been discussed by Scudder and Conelly (1985) who describe four stages in the evolution of a typical fishery — roughly corresponding to the four stages in the development of a river basin as defined in Welcomme (1979). Management needs and strategies at each of the four stages differ considerably in approach and effectiveness, particularly as the socio-economic framework of the continent is changing rapidly in many areas. Most drastic of the changes in the fisheries sector is the increasing penetration of commercial fisheries financed from urban centers into areas which were previously the domain of rural fishermen, with the consequent disruption of traditional life styles and frequently adverse effects on the fish stocks.

Catches from fisheries based on wild stocks are supplemented by a traditional, extensive aquaculture in several West African rivers (Welcomme 1971). In the Oueme, drain-in ponds are constructed on the floodplain and this technique has been transferred to the Niger and Senegal Rivers, where damming the canals draining floodplain depression lakes, retains larger areas of water on the plain through the dry season. Brush parks installed either in the channels of the river or in floodplains lakes are also widespread in West African rivers (Welcomme 1972).

Environmental damage in African rivers has so far been limited to the impacts of large dams such as Kariba on the Zambezi, Manantali on the Senegal, Kainji on the Niger, and Nasser/Nubia on the Nile. Fisheries downstream of these and other reservoirs have diminished as the floods have been altered. Some attempts have been made to improve the yields from such areas by releasing water to create artificial floods, as on the Pongolo floodplain (Coke 1970). Mitigation of the adverse effects by introduction of aquaculture associated with irrigation on the floodplain, has been suggested but have so far met with little success. The impact of further dam construction and of water abstractions for irrigated agriculture will probably increase over the next few decades to radically change the nature of African river fisheries.

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References

BAKARE, O. 1970. Bottom deposits as food for inland freshwater fish, p. 65–85. *In* S. A. Visser [ed.] Kainji Lake Studies, Vol. 1, Ecology. University of Ibadan Press, Ibadan, Nigeria.

BALOGUN, R. A. 1970. Occurrence of free amino acids and sugars in Lake Kainji, p. 103–106. *In* S. A. Visser [ed.] Kainji Lake Studies, Vol. 1, Ecology. University of Ibadan Press, Ibadan, Nigeria.

BALON, E. K., AND A. G. COCHE [ED.] 1974. Lake Kariba: a man-made tropical ecosystem in Central Africa. Monogr. Biol. 24: 767 p.

BENECH, V., AND J. QUENSIERE. 1982. Migrations de poissons vers le Lac Tchad à la decrue de la plaine inondée du Nord-Cameroun. I note — Méthodologie d'échantillonage et résultats généraux. Rev. Hydrobiol. Trop. 15(3): 191–282.

1983. Migrations de poissons vers le Lac Tchad à la decrue de la plaine inondée du Nord-Cameroun. II Note — comportement et rythmes d'activités des principales espèces. Rev. Hydrobiol. Trop. 16(1): 79–101.

1984. Migrations de poissons vers le Lac Tchad à la decrue de la plaine inondée du Nord-Cameroun. III Note — influence de l'hydrologie sur les variations interannuelles. Rev. Hydrobiol. Trop. 16(3): 287–316.

BLACHE, J. 1964. Les poissons du bassin du Tchad et du bassin adjacent du Mayo Kebbi. Mémoires ORSTOM 4: 483 p.

BLACHE, J., AND F. MITON. 1962. Première contribution à la connaissance de la pêche dans le bassin hydrographique Logone-Chari Lac Tchad. Mémoires ORSTOM 4(1): 142 p.

BLANC, M., J. DAGET, AND F. D'AUBENTON. 1955. Recherches hydrobiologiques dans le bassin du Moyen-Niger. Bull. Inst. Fr. Afr. Noire, (A. Sci. Nat.) 17: 619–746.

BORHAN, M. A. 1981. River Nile fish and fisheries. 1980. Institute of Oceanography and Fisheries. Inland waters and fish culture branch. Progress Rep. 5.

CAREY, T. G. 1971. Hydrological survey of the Kafue floodplain. Fish. Res. Bull., Zambia 3: 9–12.

CARMOUZE, J. P., J-R. DURAND, AND C. LEVEQUE. 1983. Lake Chad, ecology and productivity of a shallow tropical ecosystem. Junk, The Hague. 575 p.

COKE, M. 1970. The water requirements of Pongolo floodplain pans. Paper presented to the Republic of South Africa Water Year 1970 Convention: Water for the future. 6 p. (Mimeo)

COKE, M., AND R. POTT. 1970. The Pongolo Floodplain Pans: A plan for conservation. Pietermaritzberg, Natal Parks Board. 34 p.

DAGET, J. 1952. Mémoires sur la biologie des poissons du Niger. 1. Biologie et croissance des espèces du genre Alestes. Bull. Inst. Fr. Afr. Noire 14(1): 191–225.

1957. Données récentes sur la biologie des poissons dans le Delta Central du Niger. Hydrobiologia 9: 321–347.

1960. Les migrations des poissons dans les eaux douces tropicales africaines. Indo-Pac. Fish. Counc. Proc. 8(3): 79–82.

DAGET, J., AND P. S. ECONOMIDIS. 1975. Richesse spécifique de l'ichtiofaune de Macedoine orientale et de Thrace occidentale (Grèce). Bull. Mus. Nat. Hist. Nat. 3^e^ Sér. (Ecol. Gén. 27) 346: 81–84.

DAGET, J., AND J. -M. ECOUTIN. 1976. Modèles mathématiques de production applicables aux poissons subissant un arrêt annuel prolonge de croissance. Cah. ORSTOM (Sér. Hydrobiol.). 10(2): 59–70.

DAGET, J., N. PLANQUETTE, AND P. PLANQUETTE. 1973. Premières données sur la dynamique des peuplements de poissons du Bandama (Côte d'Ivoire). Bull. Mus. Nat. Hist. Nat. 3^e^ Sér. (Ecol. Gén. 7) 151: 129–143.

DANSOKO, F. D., H. BREMAN, AND J. DAGET. 1976. Influence de la sécheresse sur les populations d'*Hydrocynus* dans le delta central du Niger. Cah. ORSTOM (Sér. Hydrobiol.) 10(2): 71–76.

DUDLEY, R. G. 1972. Biology of Tilapia on the Kafue floodplain, Zambia: Predicted effects of the Kafue Gorge Dam. Ph. D. dissertation, University of Idaho, Moscow, USA. 50 p.

1974. Growth of Tilapia on the Kafue floodplain, Zambia: Predicted effects of the Kafue Gorge Dam. Trans. Am. Fish. Soc. 103: 281–291.

DURAND, J. R. 1970. Les peuplements ichtyologiques de l'El Beid. Première note. Présentation du milieu et résultats généraux. Cah. ORSTOM (Sér. hydrobiol.) 4(1): 3–36.

1971. Les peuplements ichtyologiques de l'El Beid. 2^e^. Note. Variations inter et intraspécifiques. Cah. ORSTOM (Sér. hydrobiol.) 5(2): 147–159.

1974. Biologie et dynamique des populations d'Alestes baremoze (Pisces: Characidae) du bassin Tchadien. Trav. Doc. ORSTOM 98: 322 p.

1978. Biologie et dynamique des populations d'*Alestes baremoze* (Pisces: Characidae) du bassin Tchadien. Trav. Doc. ORSTOM 98: 322 p.

EADIE, J. MCA., T. A. HURLY, R. D. MONTGOMERIE, AND K. L. TEATHER. 1986. Lakes and rivers as islands: species-area relationships in the fish faunas of Ontario. Environ. Biol. Fish. 15(2): 81–89.

EGBORGE, A. B. M. 1971. The chemical hydrology of the River Oshun, Western State, Nigeria. Freshwat. Biol. 1(3): 257–272.

1974. The seasonal variation and distribution of phytoplankton in the River Oshun, Western State, Nigeria. Freshwat. Biol. 4(2): 177–91.

EISMA, D. 1982. Supply and dispersal of suspended matter from the Zaire River, p. 419–428. *In* E. T. Degens [ed.] Transport of carbon and minerals in major world rivers, Part I. Mitt. Geol. -Paleont. Inst. Univ. Hamburg, No. 1.

FAO/UN. 1969. Report to the Government of Zambia on fishery development in the Central Barotse floodplain. Second phase. Based on the work of D. Duerre. Rep. FAO/PNUD (TA), 2638: 80 p.

1970. Report to the Government of Nigeria on fishery investigations on the Niger and Benue Rivers in the northern region and development of a programme of riverine fishery management and training. Based on the work of M. P. Motwani. Rep. FAO/UNDP (TA) 2771: 196 p.

1971. Rapport au Gouvernement du Dahomey sur l'évolution de la pêche intérieur, son état actuel et ses possibilités, établi sur la base des travaux de R. L. Welcomme, Spécialiste de la pêhce. Rapp. FAO/UNDP (AT), 2938: 97 p.

Fox, P. J. 1976. Preliminary observations on fish communities of the Okavango Delta, p. 125–130. *In* Proceedings of the Symposium on the Okavango Delta and its future utilization. Botswana Society: Gaberones.

Hart, R. C. 1982. The Orange River: Preliminary results. *In* E. T. Degens [ed.] Transport of carbon and minerals in major world rivers, Part 1. Mitt. Geol.-Paleont. Inst. Univ. Hamburg, No. 52.

1983. The Orange River: Supplementary results, p. 451–457. *In* E. T. Degens [ed.] Transport of carbon and minerals in major world rivers, Part 2, Mitt. Geol.-Paleont. Inst. Univ. Hamburg, No. 44.

Holčík, J., and I. Bastl. 1976. Ecological effects of water level fluctuations upon the fish populations in the Danube River floodplain in Czechoslovakia. Acta Sci. Nat. Acad. Sci. Bohemoslov., Brno. 10(9): 46 p.

1977. Predicting fish yield in the Czechoslovakian section of the Danube River based on the hydrological regime. Int. Rev. Gesamten Hydrobiol. 62(4): 523–532.

Holden, M. J. 1963. The populations of fish in dry season pools of the River Sokoto. Fish. Publ. Colon. Off. 19: 58 p.

Holden, M. J., and J. Green. 1960. The hydrology and plankton of the River Sokoto. J. Anim. Ecol. 29: 65–84.

Illies, J., and L. Botosaneanu. 1963. Problèmes et méthodes de la classification de la zonation écologique des eaux courantes, considérées surtout du point de vue faunistique. Mitt. Int. Verein. Theor. Angew. Limnol. 12: 1–57.

Kapetsky, J. M. 1974a. Growth, mortality and production in five fish species of the Kafue River floodplain, Zambia. Ph. D. dissertation, University of Michigan, MI. 205 p.

1974ab. The Kafue River floodplain: an example of preimpoundment potential for fish production, p. 497–523. *In* E. K. Balon and A. G. Coche [ed.] Lake Karibe: a man-made tropical ecosystem, in Central Africa. W. Junk, The Hague.

Kimpe, P. de. 1964. Contribution à l'étude hydrobiologique du Luapula — Moero. Ann. Mus. R. Afr. Cent. (Ser. 8 Sci. Zool.) 1287: 1–238.

Krykhtin, K. L. 1975. Causes of periodic fluctuations in the abundance of the non-anadromous fishes of the Amur River. J. Ichthyol. 15(5): 826–829.

Leopold, L. B., M. B. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. W. H. Freeman, San Francisco, CA. 522 p.

Leveque, C. 1971. Prospection hydrobiologique du lac de Lere et des mares avoisinantes. I. — Milieu physique. Cah. ORSTOM. (Sér. Hydrobiol.) 5: 161–169.

Livingstone, D. A. 1963. Data of Geochemistry. Chapter G, Chemical composition of rivers and lakes. Washington D.C., Government Printing Office. Geological Survey Professional Paper 440–S. 64 p.

Loubens, G. 1969. Étude de certains peuplements ichtyologiques par des pêches au poisson (I^{re} note), Cah. ORSTOM (Sér. hydrobiol.) 3(2): 45–73.

1970. Étude de certains peuplements ichtyologiques par des pêches au poisson (2^{e} note). Cah. ORSTOM (Sér. hydrobiol.) 4(1): 45–61.

Lowe-McConnell, R. H. 1967. Some factors affecting fish populations in Amazonian waters, p. 117–186. *In* Atas do Simposio sobre a biota Amazonia, Conselho Nacional Pesquisas, Rio de Janeiro, Consevacao de Natureza e Recursos Naturais.

1975. Fish communities in tropical freshwaters. Longman, London. 337 p.

Malaisse, F. 1969. Les facies d'un cours d'eau tropical: La Luanza (Haut-Katanga, Rep. Dem. Congo). Verh. Internat. Verein. Limnol. 17: 956–40.

1976. Écologie de la rivière Luanza. Cercle Hydrobiol. de Bruxelles: 151 p.

Martins, O. 1982. Geochemistry of the Niger River, p. 397–418. *In* E. T. Degens [ed.] Transport of carbon and minerals in major world rivers, Part 1. Mitt. Geol.-Paleont. Inst. Univ. Hamburg., No. 52.

Mefit-Babtie. 1983. Development studies in the Jonglei canal area. Final report to Government of the Democratic Republic of the Sudan. Mefit-Babtie, Glasgow, 4 Vols., 107, 273, 265, 87 pp.

Merona, B. de. 1983. Modèle d'estimation rapide de la croissance des poissons. Applications aux poissons d'eau douce d'Afrique. Rev. Hydrobiol. Trop. 16(1): 103–113.

Monakov, A. V. 1969. Zooplankton and the zoobenthos of the White Nile and adjoining waters in the Republic of the Sudan. Hydrobiologia 33: 161–185.

Novoa, D. (ed.). 1982. Los recursos pesqueros del Rio Orinoco y su explotacion. Corporacion Veneolana de Guayana, Division de desarollo agricola, Caracas. 386 p.

Odum, E. P. 1967. The strategy of ecosystem development. Science 164(3877): 262–270.

Paugy, D., 1978. Écologie et biologie des *Alestes baremze* (pisces, Characidae) des rivières de Côte d'Ivoire. Cah. ORSTOM (Sér. Hydrobiol.) 12(3–4): 245–275.

Raimondo, P. 1975. Monograph on Operation Fisheries, Mopti, p. 294–311. *In* Consultation on fisheries problems of the Sahelian zone, Bamako, Mali, 13–20 November 1974. CIFA Occas. Pap.

Rapport, D. J., H. A. Regier, and T. C. Hutchinson. 1985. Ecosystem behaviour under stress. Am. Nat. 125(5): 617–640.

Reizer, C. 1971. Contribution à l'étude hybrobiologique du Bas-Senegal. Premières recommandations d'aménagement halieutique. Nogent-sur-Marne, Centre Technique Forestier Tropical. 142 p.

1974. Définition d'une politique d'aménagement des resources halieutiques d'un ecosystème aquatique complex par l'étude de son environnement abiotique, biotique et anthropique. Le fleuve Senegal moyen et inférieur. Doctorat en Sciences de l'environnement, Dissertation, Arlon, Fondation Universitaire Luxembourgeoise. 4 vols.: 525 p.

Rzoska, J. 1974. The Upper Nile Swamps, a tropical wetland study. Freshwat. Biol 4: 1–30.

1978. On the nature of rivers with case stories of Nile, Zaire and Amazon. Junk, The Hague. 67 p.

Rzoska, J., and J. F. Talling. 1966. Plankton development in relation to hydrology and reservoir regime in the Blue Nile. Verh. Internat. Verein. Limnol. 16: 716–718.

Schlesinger, D. A., and H. A. Regier. 1982. Climatic and morphoedaphic indices of fish yields from natural lakes. Trans. Am. Fish. Soc. 111: 141–150.

Scudder, T., and T. Conelly. 1985. Management systems for riverine fisheries. FAO Fish. Tech. Pap. (263): 85 p.

Soliman, H. A. 1982. The Nile River: Study of carbon transport, p. *In* E. T. Degens [ed.] Transport of carbon and minerals in major world rivers, Part 1. Mitt. Geol.-Paleont. Inst. Univ. Hamburt, No. 52.

1983. Nile research at Asyut University, p. 385–399. *In* E. T. Degens [ed.] Transport of carbon and minerals in major world rivers, Part 2. Mitt. Geol.-Paleont. Inst. Univ. Hamburg, No. 55.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Trans. Am. Geophys. Union 38: 913–20.

Talling, J. 1957. The longitudinal succession of water characteristics in the White Nile. Hydrobiologia 9(1): 73–89.

University of Idaho, D. W. Chapman, W. H. Miller, R. G. Dudley, and R. J. Scully. 1971. Ecology of fishes in the Kafue River. Report prepared for FAO/UN acting as executing agency for UNDP. Moscow, Idaho, University of Idaho. FI:SF/ZAM 11: Tech. Rep. 2: 66 p.

UNIVERSITY OF MICHIGAN, K. F. LAGLER, J. M. KAPETSKY, AND D. J. SEWART. 1971. The fisheries of the Kafue River Flats, Zambia, in relation to the Kafue Gorge Dam. Report prepared for the FAO/UN acting as executing agency for the UNDP. Ann Arbor, Michigan, FI:SF/ZAM 11: Tech. Rep. 1: 161 p.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

VISSER, S. A. 1970. The distribution of organic compounds in freshwater lakes and rivers, p. 107–125. *In* S. A. Visser [ed.] Kainji Lake Studies Vol. 1, Ecology. University of Ibadan Press, Ibadan, Nigeria.

WELCOMME, R. L. 1971. A description of certain indigenous fishing methods from southern Dahomey. Afr. J. Trop. Hydrobiol. Fish. 2(1): 129–140.

1972. An evaluation of the acadja method of fishing as practised in the coastal lagoons of Dahomey (West Africa). J. Fish. Biol. 4: 39–55.

1976. Some general and theoretical considerations on the fish yield of African rivers. J. Fish. Biol. 8: 351–364.

1979. The Fisheries ecology of floodplain rivers. Longman, London. 317 p.

1985. River Fisheries. FAO Fish. Tech. Pap. 262: 330 p.

1986. Considerations of fish yield in rivers. Pol. Arch. Hydrobiol. 33(3/4): 305–318.

1986a. The effects of the sahelian drought on the fishery of the central delta of the Niger River., Aquacult. Fish. Manage. 17(2): 147–154.

WELCOMME, R. L., AND D. HAGBORG. 1977. Towards a model of a floodplain fish population and its fishery. Environ. Biol. Fish. 2(1): 7–22.

WHITEHEAD, P. J. P. 1959. The anadromous fishes of Lake Victoria. Rev. Zool. Bot. Afr. 59(3-4): 329–363.

WILLIAMS, R. 1971. Fish ecology of the Kafue River and floodplain environment. Fish. Res. Bull., Zambia. 5: 305–330.

WILLOUGHBY, N. C., AND D. TWEDDLE. 1978. The ecology of the commercially important species in the Shire Valley fishery, Southern Malawi, p. 137–152. *In* Symposium of river and floodplain fisheries in Africa, Bujumbra, Burundi. CIFA Tech. Pap. 5.

WIMPENNY, R. S. 1943. The fisheries of Egypt. Sci. Prog. Lond. 29 (114): 210–227.

Assessment of the Niger River Fishery in Niger (1983–85) with Implications for Management

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Abstract

MALVESTUTO, S. P., AND E. K. MEREDITH. 1989. Assessment of the Niger River fishery in Niger (1983–85) with implications for management, p. 533–544. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

From 1983 to 1985, fishing effort, fish harvest and market value of the harvest declined by 50 % along the Niger River in Niger. Strong regional contrasts were evident, as fishing effort decreased by 90 % in the southern region of the river and there were significant ($P<0.10$) differences in fishing success and the profitability of fishing between the north and south. In the south, the length frequency distribution of the catch was highly skewed toward smaller individuals and the majority of fish harvested were immature.

The depressed status of the fishery during the period of study was the result of a combination of adverse environmental conditions associated with the Sahelian drought and relatively high fishing pressure. The fish harvest of 4 000–5 000 t per annum indicative of normal flows during the 1960's would have been reduced by an estimated 40 % due to the low flow conditions. The additional reduction in harvest to less than 1 000 t per annum presently can be attributed to the effects of fishing.

Given the regional contrasts documented, it is evident that generalized concepts applicable to rivers are valuable for setting gross expectations concerning fish production, but that management of artisinal fisheries must be based on localized assessments that incorporate biological and socioeconomic considerations. Management institutions must be formulated around traditional, community-level management systems that encourage participation by fishermen in the conservation of the fish resource for their own well-being.

Résumé

MALVESTUTO, S. P., AND E. K. MEREDITH. 1989. Assessment of the Niger River fishery in Niger (1983–85) with implications for management, p. 533–544. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

De 1983 à 1985, on a observé une baisse de 50 % de l'effort de pêche, des prises et de la valeur marchande des prises le long du Niger (Niger). On a noté des différences régionales marquées : une baisse de 90 % de l'effort de pêche dans le tronçon sud du fleuve et des différences significatives ($P<0,10$) du succès de la pêche et de la rentabilité entre le nord et le sud du pays. Dans le sud, la distribution des fréquences de longueur était fortement désaxée en faveur des petits individus tandis que la majorité des poissons capturés étaient immatures.

La faiblesse de la pêche au moment de la réalisation de la présente étude était le résultat d'une combinaison de facteurs environnementaux défavorables associés à la sécheresse du Sahel et à une pression par pêche relativement élevée. Les captures annuelles de 4 000 à 5 000 t indicatrices de débits normaux pendant les années 1960, auront ainsi été réduites d'environ 40 % à cause du faible débit. La baisse supplémentaire des prises, qui s'élèvent actuellement à moins de 1 000 t par an, peut être attribuée aux répercussions de la pêche.

Étant donné les différences régionales signalées, il est évident que les concepts généraux applicables aux cours d'eau sont précieux pour ce qui est de l'établissement des prévisions globales de la production piscicole ; toutefois, la gestion des pêches artisanales doit être basée sur des évaluations locales qui tiennent compte des facteurs biologiques et socio-économiques. Les méthodes de gestion doivent être centrées sur des systèmes de gestion traditionnels au niveau des collectivités, systèmes qui encouragent les pêcheurs à participer à la conservation de la ressource pour leur propre avantage.

Introduction

Fisheries biologists working on the African continent have directed their effort primarily toward assessing the status of lake fisheries, and rivers have received relatively little attention, as is the case on a worldwide basis. Reasons for this probably reside in the open-ended nature of river ecosystems; the potential for large fluctuations in aquatic environment caused by the annual hydrological cycle; the large diversity of physical habitats that may exist with con-

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comitant adaptations by riverine fishes; and the sheer size of these systems, commonly crossing national boundries. These factors make adequate sampling, characterization and management of fisheries in rivers difficult relative to those associated with most lacustrine environments.

Fishing is the primary use of African rivers by man. The preponderance of inland fisheries are artisanal in nature, supplying families with food and income. Fishing usually is not a full-time activity, but rather is integrated into pastoral or agricultural customs which are tied to the seasonality of the flood cycle. In many cases, fishing is vital to the livelihoods of those who fish and provides high quality food and employment to others via the market system. African rivers produce 40–50 % of the fish harvest in Africa (Welcomme 1985) and fish represent about 25 % of the total animal protein consumed by the people of that continent (Shell 1986).

Fish resources are susceptible to environmental and man-induced stresses and can deteriorate rapidly, particularly when environment and man act concurrently to limit production. Generalized concepts (Vannote et al. 1980; Welcomme 1976) are valuable for characterizing riverine environments, or for setting gross expectations concerning fish production; however, management of artisanal fisheries must be conducted on a localized level. Information on the status of these fisheries must reflect conditions in a timely manner and provide a broad enough biological and socioeconomic perspective so that people can be effectively integrated into management programs.

The objectives of the study presented here were to document relationships between fishing effort, fish harvest and economic returns to fishermen regionally along the Niger River in Niger from 1983 to 1985. The summary of the data focuses on relationships between fishing effort, environment and benefits derived from the fishery. These findings are integrated with sociological information to formulate an "optimal" management plan.

Background

The Niger River is the longest river in West Africa (4 200 km) and the fourteenth longest in the world. It begins at an elevation of 800 m in the Fouta Djallon highlands of Guinea, approximately 250 km from the Atlantic coast and travels through Mali, and then into Niger, where in the south, it forms the border with Benin. After flowing through Nigeria, the river empties into the Gulf of Guinea (Fig. 1). The Niger River would be classified as a Sudanian river by Daget and Iltis (1965), as it drains an arid savannah region (the Sahel) with no fringing forest. The fish fauna is soudanian in character so that roughly one-half of the recorded fish species from the upper and middle Niger River also occur in the Nile and Gambia rivers (Beadle 1974).

During the first 1 500 km of its course, the Upper Niger flows northeast through Mali and forms a seasonally induated floodplain of about 20 000 km^2 known as the Central Delta which supports an extremely productive fishery. Welcomme (1985) reported that 90 000 t were harvested from the Central Delta in 1971. This floodplain region is vital not only to the lives of the 50 000 or so fishermen that utilize the resource, but also to the cattle-herding nomads who lead their herds to the pastures that are created anew each year as the water recedes.

North of Gao in Mali, the river bends sharply to the southeast and the Lower Niger flows to the Gulf of Guinea, largely confined to the main river channel, but with commonly occurring floodplains. The only mainstream impoundment is Lake Kainji in Nigeria, created in 1968 and located about 1 200 km from the mouth of the river. There are four small tributary dams in the Upper Niger system, the major one being the Selingue Dam on the Sankerani River in Mali which provides about 50 000 ha of irrigated area (Drijver and Marchand 1985).

The 575 km of river in Niger can be classified into three distinct ecological zones: (1) The section of the river from the Malian border south to the confluence with the Sirba River, characterized by a broad, internally braided floodplain, which contributes about 30 % to the length of river in Niger; (2) a central section from the Sirba River south to the confluence with the Mekrou River, with a well defined main channel and little floodplain development, representing about 45 % of the river length in Niger; and (3) the section of the river from the Mekrou to the southern border with Nigeria, about 25 % of the river length, characterized by a broad fringing floodplain primarily in Benin territory along the southwestern border of Niger (Fig. 1).

Since the late 1960's, the annual cycle of flood in the Niger River has been progressively changing such that the peak and duration of the flood is now much depressed. Figure 2 shows three patterns of flood for the river in Niger. The 1963–64 curve represents an average flood year before the advent of the drought in 1973–74. The 1973–74 curve depicts the water level regime during the initial year of the drought, which was very similar to the situation in 1985–86, for which a partial year is shown. Extremely severe conditions existed in 1985 when the river reached zero flow in May.

There are periodic descriptions of the fishery on the river in Niger from the early 1960's until 1980, but methods of estimation were different and the accuracy of the values is questionable. The work done during the 1960's by Daget (1962) and Dobrovici (1971) suggest that during that period, there were roughly 1 500 active fishermen with an associated annual harvest of 4 000–5 000 t, giving a catch per fishermen per annum of 2.7–3.3 t. Niger government figures for 1978 give an annual harvest of about 5 000 t, but it is likely that this was a perpetuation of earlier figures and no estimate of fishing effort was given. In 1980, Sheves (1981) estimated that there were 2 600 fishermen operating on the river and induced, through an economic evaluation of fishermen's households, that the harvest per fishermen per year was about 1 t, giving a total harvest estimate of 2 600 t. Relating the generalized situation in the 1960's to the figures of Sheves (1981) suggests that fishing effort doubled during the 1970's with an associated decline in harvest per canoe. The influx of people to the river basin area was a consequence of the drought; thus, as fishing effort was increasing, the flows in the river were decreasing. By the early 1980's effort had peaked and flows were severely depressed. This was the situation at the outset of the study reported here.

Materials and Methods

Fishery assessment information was collected using three independent sampling efforts: (1) a catch assessment survey

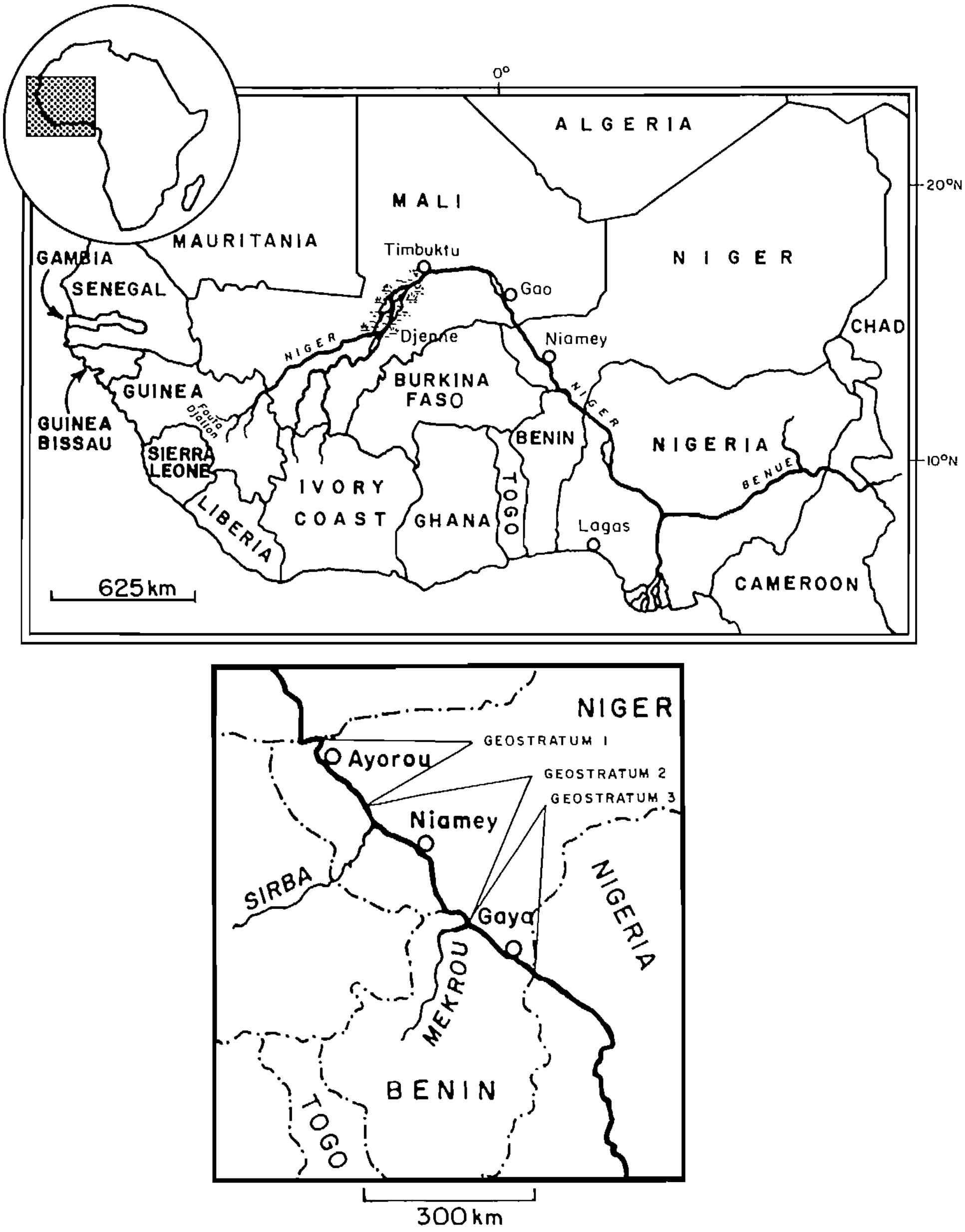

FIG. 1. Regional location of Niger River and locations of ecological zones and sampling strata for the river in Niger.

(CAS) which was conducted from March 1983 – December 1985; (2) a fish biology survey (FBS) conducted from April 1984 – December 1985; and (3) a socioeconomic survey (SES) of households conducted from April 1985 – February 1986.

Spatially, the 575 km of river in Niger was stratified from north to south into three geographical strata (geostrata):

stratum #1: Mali border to Tillaberi (125 km);
stratum #2: Tillaberi to the Mekrou River (295 km); and
stratum #3: Mekrou River to the Nigerian border (155 km).

These three goestrata largely coincide with the ecological zones of the river described in the background statement. From north to south, these geostrata will be referred to as #1 (northern, with Ayorou as the major town), #2 (central, with the capital Niamey as the major town), and #3 (southern, with Gaya as the major town) (Fig. 1).

Based on normal river flow data, the hydrological year was divided into four temporal strata (hydrostrata) as follows: 24 February–6 May (falling water = 72 days), 7 May–17 July (low water = 72 days), 18 July–27 September (rising water = 72 days), and 28 September–23 February (high water = 144 days).

All three surveys were tied to the regional and seasonal stratification given above. Because the CAS was the initial survey to be implemented, it formed the basis of the randomized sampling program. Simple random sampling was used to choose the days during which interviews would be taken within any given geo/hydrostratum unit. An average of 22 days was sampled within each unit over the 3-yr study for a total of 1 069 sampling days over the entire survey period. The review of methods to follow treats the CAS, FBS and SES in that order.

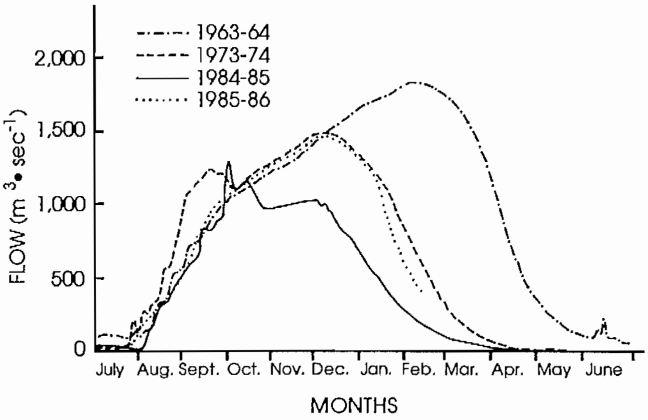

FIG. 2. Flow regimes for normal flood year (1963–64) and three low flow years representative of drought conditions for the Niger River in Niger.

Catch Assessment Survey (CAS)

At the fish landings randomly chosen for the CAS, all active fishing canoes were counted to provide an estimate of total fishing effort at any particular landing during the sample day. Interviews were taken using a standard interview schedule and each fisherman's catch was enumerated down to the species level if possible. Fish that were <25 cm total length were measured to the nearest cm and those >25 cm were measured to the nearest 2 cm. Fish that were <1 kg were weighed to the nearest 10 g, and, in general, those fish >1 kg were weighed to the nearest 50 g. If fishermen were too numerous for a total enumeration, then they were interviewed as time and manpower permitted. Canoe catches were pooled to give an estimate of catch per unit effort (kg per canoe) for the landing for that day, which was taken as being representative of the entire geographical stratum.

Effort at each landing was multiplied by catch per unit effort to give an estimate of the harvest at that landing on that day. Both effort and harvest were expanded upward using the appropriate sampling probabilites to give estimates of total effort and total harvest for the entire geostratum for that day. Mean daily values of effort (EDAY), catch (CDAY) and catch per unit effort (UDAY) were calculated for each geo/hydrostatum and expansions to seasonal and annual totals were conducted as per any stratified random sample (Bazigos 1974). Temporal and spatial comparisons of CAS data were conducted with ANOVA using the appropriate design model and null hypotheses were tested at alpha=0.10.

As part of the CAS interview schedule, each fisherman was asked to describe the fishing gear that he was using; additionally, any gear in his canoe was recorded by the fishery monitor. To estimate the proportion of the harvest going to market for sale vs to households for consumption, fishermen were asked to separate their catches into two groups and the groups were processed separately by the monitors. During the 3-yr study period, 4 014 interviews were taken.

Fish Biology Survey (FBS)

The FBS began during the falling water season of 1985 and ended during the high water season of that same year. The primary objective of the survey was to ascertain the sizes at maturity for the most important commercial fish species. Fish for this analysis were collected from experimental netting and at landings where women buyers cleaned fish before further sale. Sampling at landings was tied to the randomized design for the CAS, whereas samples from experimental netting came primarily from the northern geostratum where nets were set during 120 nights.

Sex and maturity were determined by visual observation of the gonads. Maturity was ranked as 1 (sex not visually discernable); 2 (immature — sex discernable, but gonads translucent); 3 (maturing — testis white, ovaries with eggs); 4 (mature and in spawning condition — running eggs or milt); or 5 (spent — gonads empty and flacid, much vascularization). The adult stock of a particular species was considered to represent all individuals equal to, or larger than, the smallest fish collected at maturity stage 4.

The experimental gill netting also was conducted to determine gill net selectivity characteristics applicable to the river fishery in Niger. The fishermen do not mount their nets in the standard fashion with the lumen of the meshes hanging in a vertical direction, but rather turn the meshes 90 degrees so that the long axis of the lumen is horizontally-oriented. The selectivity characteristics of gill nets mounted in this traditional way were determined by using nets composed of 23, 30, 50, and 60 mm bar mesh sizes.

Socioeconomic Survey (SES)

The SES was based on interviews from 513, or about 43 %, of the estimated 1 200 households currently engaged in fishing along the river in Niger. For efficient use of time and man-power, households were sampled using the same randomized sampling scheme used for the CAS. Generally, to interview household members, the CAS survey team would go to the village associated with a randomly chosen landing the afternoon before the day of the landing sample. The survey team met with the village chief to explain the objectives of the survey and to gain permission to interview village members. The chief usually would call the village together to explain what was going to happen and the survey team could, at that time, get a list of all village households. Three households then would be chosen at random to receive the SES interview schedule.

The interview schedule was pre-tested during October and November 1984. The focus of the questions was to evaluate benefits received from fishing relative to other activities, and to characterize fishing in economic terms at the household level. Information relevant to the assessment presented here includes monetary return from the sale of fish vs other commodities, capital investment in fishing, and expenditures for food in weekly markets.

As part of the economic characterization of the fishery, market values of fresh fish harvested were generated as if the entire harvest was sold in the market place according to the government of Niger (GON) pricing system. In actuality, some of the harvest was consumed directly in the households and some was turned into other product forms for eventual sale in markets in Niger and in neighboring countries, particularly Benin, Nigeria and Mali.

The GON fixed prices for fresh fish were tied to fish size and quality as follows:

TABLE 1. Percentage species composition of the harvest by number and weight for each geostratum (1984–85 pooled).

	Geostrata					
	I		II		III	
Species or species group[a]	No.	Wt.	No.	Wt.	No.	Wt.
Hyperopisus bebe occidentalis	—	2.8	—	—	—	—
Mormyrus rume	2.1	2.8	—	2.5	—	—
Marcusenius senegalensis pfaffi	2.3	—	—	—	—	—
Campylomormyrus tamandua	2.3	—	—	—	—	—
Alestes spp.	—	—	4.5	—	—	—
Alestes dentex	—	—	—	—	—	2.0
Alestes baremose	—	—	2.1	—	—	—
Alestes nurse	—	—	—	—	2.5	—
Citharinus citharus	—	—	—	—	6.0	2.7
Labeo spp.	—	2.8	2.1	2.3	—	—
Labeo senegalensis	5.4	6.3	5.3	6.9	7.7	9.6
Labeo coubie	2.9	6.7	2.1	3.6	—	2.1
Clarias spp.	—	—	—	2.3	4.2	3.5
Clarias anguillaris	—	3.8	2.1	4.1	2.9	5.4
Heterobranchus bidorsalis	—	2.9	—	—	—	—
Eutropius niloticus	4.0	—	—	—	—	—
Schilbe mystus	—	—	2.7	—	—	—
Bagrus spp.	—	—	—	2.8	—	—
Bagrus bayad macropterus	—	—	—	2.3	—	3.5
Bagrus docmac niger	—	3.7	—	2.4	—	—
Chrysichthys spp.	—	—	2.8	—	—	—
Chrysichthys auratus longifilis	3.7	—	—	—	—	—
Chrysichthys nigrodigitatus	2.1	2.0	—	2.6	3.0	4.9
Synodontis spp.	3.8	2.4	11.7	5.9	7.0	3.5
Synodontis violaceus	3.5	—	—	—	—	—
Synodontis schall	14.8	7.4	8.4	4.2	4.2	3.5
Sarotherodon galilaeus	6.7	3.1	4.0	2.2	12.2	6.0
Oreochromis niloticus	6.3	4.4	4.2	2.7	21.0	11.7
Tilapia zillii	3.6	—	2.1	—	4.9	2.5
Lates niloticus	—	11.9	—	8.7	—	2.8
Total %	63.5	63.0	51.4	57.7	75.6	63.7
Total no. of spp. that occurred	123		162		94	

[a]Species groups, e.g. *Alestes* spp., represent all individuals of that genus that could not be identified to species level.

population composed of larger individuals. In general, based on the community length frequency distributions, 74 % of the fish harvested in the southern region were less then 20 cm total length, whereas the value was 34 % in the northern area.

Further contrasts between the northern and southern regions of the river were evident when the length structures of the principal species were analyzed with reference to their sizes at maturity. Table 2 gives the lengths at which 30 % (L30) of the adult stocks had reached maturity based on samples taken during 1984 and 1985. The L30 gave reasonable lengths at maturity relative to those in the literature over the range of small to large species in the fish community. In the southern stratum, a larger proportion of the fish harvest was composed of immature individuals; for example, over 90 % of the harvest of one-third of the major commercial species was composed of immature fishes. In the northern stratum, there were no species where the percentage of immature individuals exceeded 90. In the southern area, fully 98 % of the nile perch harvested were immature, whereas the percentage was 46 in the northern stratum.

TABLE 2. The total lengths (cm) at which 30 % (L30) of the adult fish of the commercially important species reached maturity (gravid condition) in 1984–85. An adult of a given species was defined as any fish longer than the smallest gravid individual observed.

Species (groups)	Number of adults sampled	L30
Hyperopisus bebe occidentalis	26	36
Mormyrus rume	95	36
Mormyrops spp.	37	40
Hydrocynus spp.	104	26
Labeo senegalensis	202	28
Labeo coubie	53	38
Clarias spp.	46	26
Eutropius niloticus	725	21
Bagrus bayad macropterus	23	48
Bagrus docmac	11	36
Chrysichthys auratus longifilis	95	18
Chrysichthys nigrodigitatus	17	37
Auchenoglanis spp.	31	33
Hemisynodontis membranaceous	148	34
Synodontis schall	273	20
Sarotherodon galilaeus	107	18
Oreochromis niloticus	263	20
Lates niloticus	72	42

Gear Composition and Selectivity

If differences in fish community size structures between the northern and southern regions are truly related to fishing pressure, then there should be a contrast in gear composition between the two regions of the river, with the southern region showing a stronger tendency toward gears that harvest smaller sizes of fish. Table 3 shows that gear composition changed significantly ($P < 0.10$) over the course of the study in both regions and that the trend was toward increased use of smaller mesh sizes. The shift was stronger in the south where relative use of 40-mm mesh decreased by 40 %, while that of 30-mm mesh increased by 96 %. In both sections, the strong shifts in gear composition occurred from 1984 to 1985. In 1985, fishermen were using a significantly ($P < 0.10$) higher complement of 20- and 30-mm mesh nets in the south than in the north, although 30-mm was the predominant mesh in both places, most likely because it was the minimum legal mesh size in effect during the study.

Cast nets also were an important component of the fishing gear in use on the river. There was no significant change ($P > 0.10$) in the relative use of gill nets and cast nets over the 3-yr study period for the river as a whole. There was a significant difference ($P < 0.10$), however, in the relative abundance of these gears between the northern and southern strata. For the study period as a whole in the north, gill nets

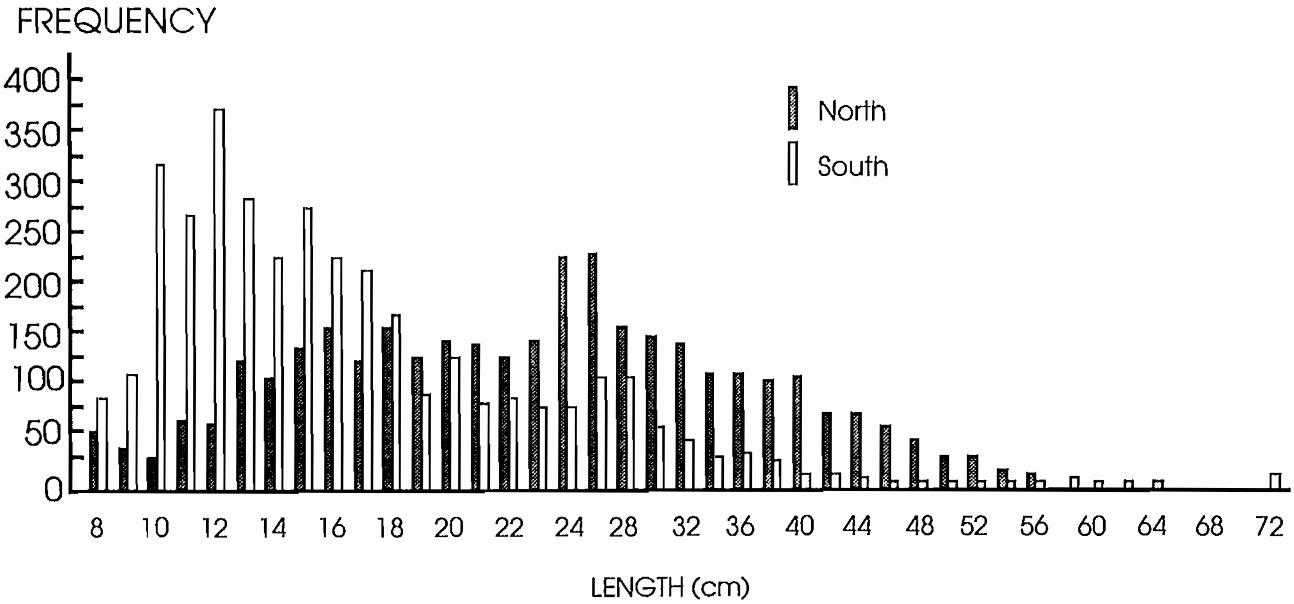

FIG. 6. Fish community length frequency distributions of fish harvested during 1984–85 from the extreme northern and southern regions of the Niger River in Niger.

TABLE 3. Mesh size composition of gill nets (% total number) for the three most commonly used meshes (bar measure) in the northern and southern geostrata of the Niger River in Niger (1983–85).

Year	Mesh size 20 mm	 30 mm	 40 mm
	Northern geostratum		
1983	3	28	32
1984	3	28	32
1985	3	39	24
	Southern geostratum		
1983	13	27	25
1984	14	30	32
1985	14	53	15

made up 75 % of the gear in use and cast nets contributed 23 %; in the southern stratum, gill nets made up 53 % of the gear in use and 39 % was attributable to cast nets.

The data on gill net selectivity acquired from the experimental gill netting was limited. Sample sizes were too small to determine selectivity characteristics of traditionally mounted nets on a per species basis. The best information was forthcoming by combining all species and obtaining selectivity ranges applicable to the entire fish community. The 50 % selectivity ranges (cm) for the fish community for certain bar mesh sizes (mm) of gill nets mounted in the local fashion were: 23 mm (18–21 cm); 30 mm (21–27 cm); 50 mm (28–41 cm), and 60 mm (34–47 cm). Information collected from interviews, where fishermen reported that their harvest came only from cast nets with mesh sizes less than 30-mm, showed that 80 % of the fish captured were less than 20 cm in total length.

If fishing pressure in the southern part of the river prior to this study was high enough to influence fish community structure, then the gear selectivity characteristics, taken with the gear composition information, imply that heavy selection pressure has been placed on fish less than 27 cm in total length in the south. The fish community length frequency distribution for the southern stratum supports this implication and Fig. 6 shows a strong decrease in the abundance of fish after about 18 cm, which might suggest strong exploitive pressure by cast nets. The length frequency distribution for the northern stratum shows a steady decline in abundance, starting at about 28 cm, which corresponds in general to the gears that were in use as described above.

The length structure, gear selectivity and length at maturity information, when combined with the earlier assessment of the fisheries to the north (geostratum #1) and to the south (geostratum #3), suggest that the southern region has been heavily fished in the recent past. The fish stocks in this area were extremely skewed toward smaller, immature fishes and the community biomass was relatively low, as indicated by the low fishing success (2.7 kg•FEU^{-1}•d^{-1}). The gill nets in use primarily captured fish smaller than the L30 over a broad range of species. In the north, the proportion of the harvest composed of mature fish was acceptable for most important species. The daily catch per canoe of between 3.5 and 4.0 kg in 1985 was evidently high enough to attract more fishing effort; however, over the study period, fishermen were striving to increase their catches in the north by use of smaller mesh sizes and fishing success significantly declined ($P<0.10$) in 1985 in that region (Fig. 5).

The situation documented during this study was logically dependent on conditions that existed on the river during previous years. Thus, a better interpretation of study results can be gained by reference to historical information. Dobrovici (1971) estimated that there were about 1 200 fishermen on the river in Niger in 1969, of whom 700 were residents and the remainder were migratory, primarily from Nigeria. Fully 570 of the 700 resident fishermen operated in the southern region with the remainder spread, in a progressively decreasing manner, northward along the river. At that time, north of Niamey, there were roughly 200 migratory fishermen and only 8 residents. Taking all

Quality class 1 (1 250 CFA/kg):	fish >1 kg in size, generally including *Lates, Mormyrus, Gymnarchus, Distichodus, Bagrus, Tilapia*);
Quality class 2 (850 CFA/kg):	fish <1 kg and >400 g, all species including larger Clariidae; and
Quality class 3 (450 CFA/kg):	fish <400 g, all species.

Although exchange rates fluctuated widely during the study period, 400 CFA (Central African Francs) per U.S. dollar will be used as a reasonable figure for presentation of dollar values. Fresh fish market value was estimated by partitioning the weight frequency distribution of total annual harvest into the above size classes and then multiplying each total class weight by the appropriate fixed market price.

Results and Discussion

This section is subdivided primarily to emphasize four major points with respect to assessment and management of the Niger River fishery in Niger: (1) Strong contrasts in characteristics of the fishery occurred regionally along the river; (2) The capacity of the riverine fish resource to respond positively to fishing pressure has been adversely affected during the Sahelian drought; (3) Socioeconomic information collected from households allowed a better understanding of the role of fishing as a household enterprise and of decision-making by fishermen; and (4) Viable management must be sociologically sensitive, and workable approaches must be an effective combination of localized, community-level control and government participation.

Assessment of the Fishery

Fishing Activity

Fishing activity, measured as the mean number of canoes in operation per day (EDAY), decreased significantly ($P<0.10$) over the period of study, from 1 300 in 1983, to 900 in 1984, to 650 in 1985. These daily values translated to total annual estimates of 475 000 canoe-days in 1983, 330 000 canoe-days in 1984 and 240 000 canoe-days in 1985. The overall decline in daily fishing effort over the 3 study years expressed on a per hectare basis using a low water surface area of 30 000 ha (Dobrovici 1971), was from 0.04 to 0.02 canoes. Thus, for the river as a whole, fishing effort decreased by 50 % over the period of study.

Figure 3 shows that the same general trend occurred regionally within each geostratum; however, the rates of decline significantly differed ($P<0.10$). The most apparent inconsistency was associated with the southern geostratum (#3) where fishing effort dropped by 90 %; the decrease was about 38 % in the other two regions.

Although total fishing effort progressively decreased in all geostrata over the period of study (Fig. 3), the numbers of local fishermen and migratory fishermen from Mali increased in the northern region in 1985, by 44 and 19 %, respectively. It is certainly likely that the number of local fishermen in the north was augmented by those who abandoned the fishery in the south. It is noteworthy that these increases in fishing effort were the only ones measured over the 3-yr period of study and only occurred in the most northern region of the river around Ayorou (Fig. 1).

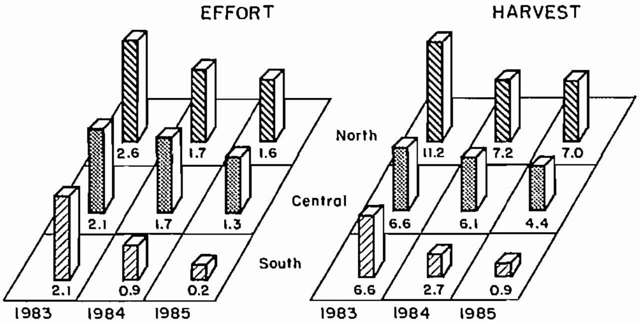

FIG. 3. Estimates of fishing effort (canoes•km^{-1}•d^{-1}) and harvest (kg•km^{-1}•d^{-1}) from 1983–1985 for each geostratum on the Niger River in Niger.

Fish Harvest

As per the trend in fishing effort, fish harvest declined significantly ($P<0.10$) over the study period. Mean daily harvest (CDAY) decreased from 4.5 t in 1983, to 3.2 t in 1984, to 2.4 t in 1985. These daily means translated to annual estimates of total harvest of 1 600 t in 1983, 1 200 t in 1984, and 900 t in 1985. On a per hectare basis, the trend over the study period represented a decline from about 50 kg•ha^{-1} in 1983 to 30 kg•ha^{-1} in 1985. Thus, the overall decrease in harvest during the 3-yr study period was 44 % which corresponded closely to the 50 % decrease in fishing effort over the same period.

The pattern of annual decline in harvest for each geostratum was very similar to the pattern for fishing effort (Fig. 3). The strong relationship between harvest and fishing effort during the study period is illustrated in Fig. 4, which shows the significant ($P<0.10$) linear regression ($r^2=0.81$) of harvest on effort. The data are expressed on a per kilometer basis and represent the 36 geo/hydrostratum combinations (12 per year) sampled over the 3-yr period. Thus, despite annual hydrological cycles, geographical differences in river morphology, and a progressive decrease in flows over the study period, the magnitude of harvest was largely explained by the number of canoes in operation.

When the residuals of the regression relationship shown in Fig. 4 were subjected to ANOVA using hydrostrata and geostrata as sources of variability in the design model, geostrata explained a significant portion (20 %) of the residual variance. This implies that, over and above fishing effort, variation in harvest was more associated with geographical factors than with hydrological changes over the 3-yr period. The inclusion of mean daily water level in a multivariable model after taking fishing effort into account did not improve the relationship significantly.

Fishing Success

The daily harvest per canoe (UDAY) is a measure of fishing success for the average canoe, or fishing economic unit (FEU), and is influenced primarily by the catchability and

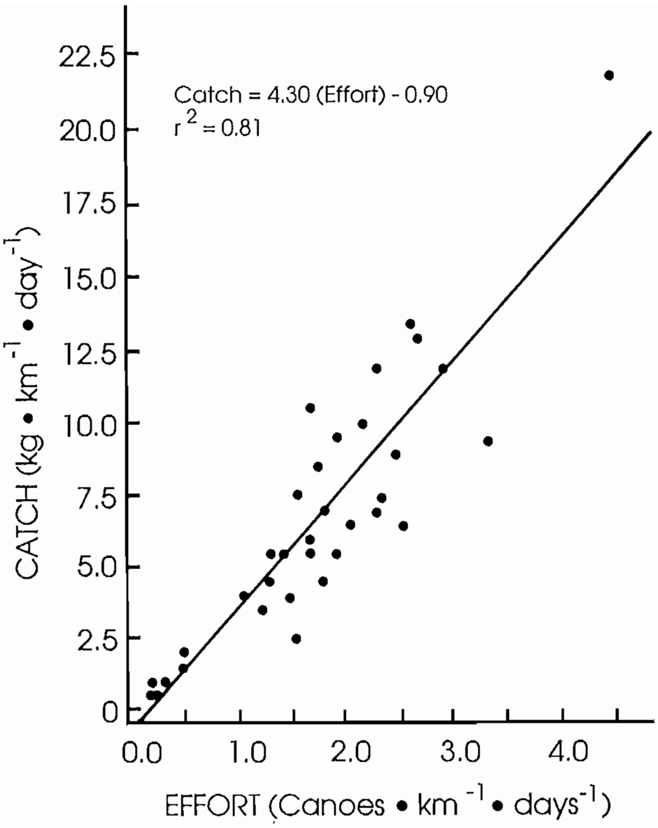

FIG. 4. Regression of harvest (kg•km^{-1}•d^{-1}) on fishing effort (canoes•km^{-1}•d^{-1}) using estimates from the 36 geo/hydrostrata combinations encompassed in the 3-yr study on the Niger River in Niger.

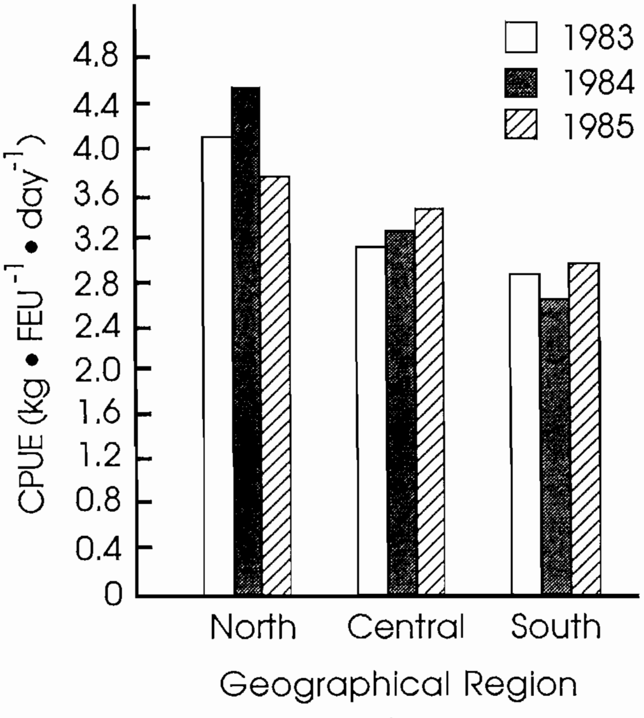

FIG. 5. Estimate of CPUE (kg•FEU^{-1}•d^{-1})from 1983 to 1985 for each geostratum on the Niger River in Niger.

abundance of fish. Taking the river as a whole, fishing success was constant over the 3 years of study at 3.3 kg•FEU^{-1}•d^{-1}. Figure 5 shows, however, that when viewed on a geographical basis, there were significant differences ($P<0.10$). Based on annual averages, fishing success was highest in the north (4.1 kg•FEU^{-1}•d^{-1}), intermediate in the central region (3.2 kg•FEU^{-1}•d^{-1}) and lowest in the south (2.7 kg•FEU^{-1}•d^{-1}). The average daily difference per canoe of 1.4 kg between the northern and southern regions represented a difference in total annual harvest of about 500 kg. As Fig. 5 illustrates, the average annual values of UDAY varied little from year to year within geostrata. In 1985, however, there was a significant ($P<0.10$) decrease in UDAY in the northern geostratum.

Over the 3 years of study, then, fishing effort decreased significantly, particularly in the most southern region, as did harvest. Fishing success, however, remained relatively constant for those who did continue to fish. Geographical differences in effort, harvest and fishing success suggest that regions of the river can function relatively independently of one another, and that whole-river values may not be representative of localized situations. There were strong contrasts between the most southern region of the river, where fishing success was the lowest and where the strongest decline in fishing effort occurred, and the most northern section of the river, where fishing success was the highest and where local and Malian fishing effort increased in 1985.

Harvest Composition

The species composition of the harvest remained relatively stable over the period of study, but varied somewhat between geostrata. Table 1 gives the species composition of the harvest by number and weight for species that contributed >2 % during 1984 and 1985 combined, the years when fish taxa were most appropriately identified by field personnel. The table shows that the genera most consistently represented regionally along the river were *Labeo, Synodontis* and two species of cichlids, *Sarotherodon galilaeus* and *Oreochromis niloticus*. The synodontids dominated as a group in the northern region and contributed 22 % by number to the harvest in that area. In the southern region, dominance shifted to the cichlids which made up 38 % of the harvest by number. Nile perch (*Lates niloticus*), though not important by number, contributed the most to weight of fish harvested in the northern and central sections of the river, but were a minor component in the southern region. Based on the total number of species represented in the harvest from the three geostrata, fish diversity was highest in the central region (162 species), intermediate in the north (123 species) and lowest in the south (94 species). For each region, the few species listed in Table 1 (< 15 in all cases) comprised the majority of the harvest.

Size Structure of the Harvest and Fish Maturation

There were strong north-south contrasts in the length structures of the fish communities (Fig. 6). For most species in the southern region, there was a knife-edge mortality over a narrow range of lengths, after which, larger individuals were rare. In the northern area, the length structure was more evenly distributed, with a greater proportion of the fishermen into account, Dobrovici (1971) estimated the density on the river in the southern region to be about 17 times that in the northern area. The fishermen were using gill nets of mesh sizes primarily between 40 and 80 mm bar mesh. It is evident that in the late 1960's and early 1970's, fishing pressure was predominately concentrated in the southern region and that the gill net users were directing their effort at larger-sized fish.

In 1980, Sheves (1981) estimated the total number of fishermen on the river in Niger to be 2 600. If our values are converted from canoes to fishermen, then the effort in 1983 was about 2 500 fishermen. Thus, effort was about twice as high in the early 1980's as in the early 1970's, although by 1983, fishermen were well dispersed along the river and the density of canoes was even slightly higher to the north around Ayorou (Fig. 3). The canoe density in 1983 was estimated to be 4 canoes per km^2, about three times the optimum density determined through empirically derived surplus yield curves for African rivers (Welcomme 1978). The estimates of fishing pressure given here for the southern region do not incorporate the contribution of the Beninoise fishermen to the total fishery in that area. Fishing effort in the southern geostratum could have been 60 % higher considering the Beninoise contribution.

Environmental Effects

The discussion heretofore has emphasized the contrast between the northern and southern regions of the Niger River in Niger to demonstrate that fishing pressure most likely has influenced the structure and dynamics of the fish stocks. There are certain aspects of the fish communities in relation to their environment, however, that may have contributed to the effects of fishing in these two areas. The river above Ayorou leads north into Mali to large, fringing floodplains near Gao and eventually to the Central Delta. These productive areas may serve as sources of continual recruitment for the northern river area in Niger, which might allow that fish community to sustain itself better under intense fishing pressure. The southern ecological zone, on-the-other-hand, with localized, fringing floodplains that are annually exposed and inundated, would likely represent a more self-contained system where immature and adult fishes alike would be constantly exposed to fishing pressure and be more susceptible to fishing mortality. The higher proportion of immature fish in the harvest in the southern region may be evidence of this. The low flow regime in effect over the period of study would tend to create a more lacustrine environment, favoring proliferation of the cichlids, particularly in the absence of predators, which may explain the very high proportion of this family in the harvest from the southern geostratum (Table 1).

The Sahelian drought undoubtedly has had severe effects on the river fishery. The most relevant evidence in support of this was presented by Welcomme (1985) who correlated a 20-yr series of discharge data for the Niger River with fish landings at Mopti in Mali. The resulting multiple regression equation had a high degree of predictability ($R^2 = 0.87$) when the catch in one year was regressed against hydrological indices for the two previous years. Catches were positively correlated with flows with the implication that higher flows inundated more floodplain area which, in turn, enhanced reproductive success and survival of young fish. The increased abundance was then manifested in the catch one to two years later. Welcomme (1976) also showed that deviations from catches predicted by his generalized river model, using main channel length as the predictor variable, were largely explained by the extent of floodplain area associated with the particular river in question. Thus, it is certain that the carrying capacity of the Niger river has been reduced under the low flow conditions.

If hydrological data for the Niger River taken at Niamey from 2 normal flow years (1963 and 1964) are placed into Welcomme's (1985) linear model based on discharge data and catches for the Niger River, and the predicted catch is compared to that generated from the model when low flow data (1982 and 1983) are included, then the predicted decline in harvest is about 40 %. This decline might be viewed as the expected drop in yield due to environmental changes. These results imply that the general levels of harvest of 4 000–5 000 t which occurred in the 1960's during normal flow years (Daget 1962; Dobrivici 1971) might have decreased to roughly 2 500 t due to the depressed flows, but not down to below 1 000 t as measured in 1985.

It is reasonable that the severe decrease in yields indicative of the 1980's has been a result of depressed flows coupled with relatively high levels of fishing effort. Fish communities in rivers have the ability to support heavy fishing pressure, but it is when environmental stresses mount, that fishing pressure may cause a collapse in the fishery (Welcomme 1979). Figure 7 illustrates possible surplus production functions for prolonged high and low flow regimes for riverine fisheries. It is easy to envision that fish populations become more susceptible to fishing pressure under prolonged low flow conditions; lower flows concentrate fish for easier accessibility by fishermen and hamper movement into or out of heavily fished areas. During high water, fish are more dispersed such that catchability decreases, fishing success decreases, and in response, fishermen reduce their effort. Thus, there is a degree of fishing autoregulation built into the normal annual flood cycle.

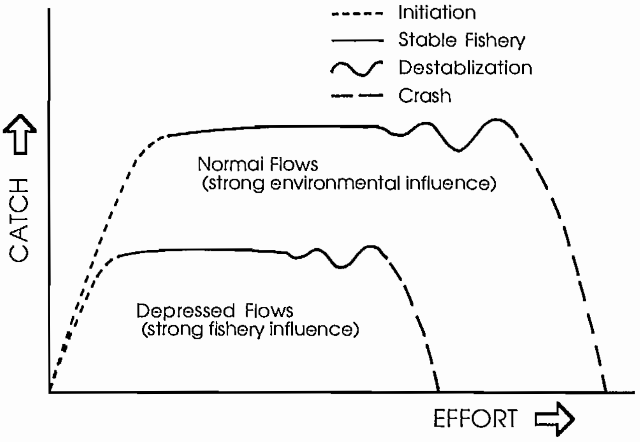

FIG. 7. Conceptual model of the possible effects of depressed flows on fish harvests from African floodplain rivers. Adapted from Welcomme (1985).

It is likely that the fishery described in this study, though severely depressed relative to pre-drought years, was in the initial stages of recovery, made possible by the reduction in fishing effort. The fishery exhibited the characteristics of the initiation phase of fishery expansion as depicted in Fig. 7, with a strong positive relation between harvest and fishing effort (Fig. 4). However, under continued low flow conditions, a high degree of protection is warrented to preserve the productive capacity of the resource. The current importance of protective measures to insure the viability of fishing as a household enterprise is further illustrated in the following two sections.

Economic Perspective

Whole-River Considerations

The market value of the fresh fish harvested from the Niger River in Niger was estimated to be 925 million CFA ($2.3 million) in 1983, 770 million CFA ($1.9 million) in 1984, and 525 million CFA ($1.3 million) in 1985. The market value of the harvest thus declined 43 % over the period of study. Based on our best estimate of 250 CFA ($0.63) for the bank-side value to the fishermen of a kilogram of fresh fish, returns to fishermen were equivalent to roughly 40 % of the market value of the harvest, and in 1985, this represented 82 % of the household income of families fishing along the river in Niger.

For households engaged in fishing, food for family consumption was derived from agricultural enterprises, although 15–25 % of the fish harvest was funneled directly into households for consumption. This household-directed harvest amounted to approximately 180 t of fish in 1985 with a market value equivalent to 81 million CFA ($200,000), using a market value of 450 CFA ($ 1.13) per kilogram, which was appropriate for the lowest quality fish (see methods). This amount translated to about 67,500 CFA ($169) when averaged on a per family basis. It was estimated that households spent an average of 4,000 CFA ($10) per week on food in the market place, so that families were choosing to consume fish with a potential market value equivalent to 32 % of their annual household food expenses. Families fishing along the river during the study must have valued fish in their diet at least as much as other things that the foregone money could have purchased.

Over and above the economic value of the food taken into the households, it would be extremely desirable to analyze the nutritional role of fish consumed. Decisions by fishermen to participate in the fishery may well be based on nutritional requirements and the availability of alternate food sources. It is certainly possible that during the drought, families were consuming the maximum amount of their catch possible given their monetary needs and the productive capacity of the resource.

Profitability of Fishing as a Household Enterprise

The declines in fishing effort documented during this study stem from decisions by the fishermen to fish less frequently, or perhaps not to fish at all. The benefits received from fishing must have been inadequate to compensate for the investment of time, energy, and money. The return on investment from fishing was 5:1 in the north and 4:1 in the south in 1985. These gross profit margins were not poor, and do not satisfactorily explain the decline in fishing activity measured over the study period. It must be remembered, however, that the socioeconomic status of households measured in 1985 was a reflection of the situation at the tail-end of the study and is applicable to the fishermen who remained in the fishery, not to those who left during the preceeding years.

Mean daily harvest per canoe (UDAY) was constant within geostrata over the 3-yr period of study (Fig. 5), and, as such, was a poor indicator of responses by fishermen to the bioeconomic status of the fishery. Given the strong contribution (82 %) that fishing made to the household incomes of the fishing communities along the river, it is reasonable to assume that decisions by fishermen concerning participation in the fishery were primarily economically motivated. A better understanding of fishermen's interactions with the resource might be forthcoming through derivation of fishery descriptors that combine both biology and economics (and ultimately other values).

We found it informative to express trends in fishing success relative to the profitability of the fishing enterprise. Given the costs associated with fishing along the river, and also considering the portion of the harvest going directly to the households (20 %), a fishermen had to harvest and sell about 0.7 kg of fish per day to break even. Fishermen might be sensitive to the proportion of the time that they do, or do not, catch enough fish to cover their investments in fishing. For the case under study, any day during which a fisherman harvested less than say, 0.75 kg, he did not cover his investment in fishing and experienced what might be called a ''no-profit day.''

The percentage of no-profit canoe-days, calculated as the percentage of all canoe fishermen interviewed who had captured less than 0.75 kg, was found to be sensitive to changes in annual fishing activity. For example, the percentage of no-profit days in the northern area around Ayorou steadily increased from 9 % in 1983 to 19 % in 1985. This is further evidence that although the northern fishery historically had not been fished as heavily as that in the south, economic viability was gradually declining, as was total fishing effort. In the southern region, however, the trend was just the opposite: the percentage of no-profit days steadily decreased from 21 % in 1983 to 12 % in 1985. It is certainly not reasonable to assume that this percentage was dropping because fishing was getting better — fishing success remained constant over the study period in the southern geostratum (Fig. 5). It is logical to assume, however, that those fishermen who left the fishery were the less successful ones, so that through their absence, the fishery as a whole functioned more efficiently on a per fishing unit basis, and the no-profit days decreased over time. Given the general scenario that a fishery will continue to expand until it reaches the economic breakeven point, or zero-rent equilibrium, it is possible that the percentage of no-profit days could have been substantially higher in the southern region in the recent past, before the onset of the dramatic decline in fishing effort documented during this study.

It is noteworthy that if the net profit differential between the northern and southern regions of the river is converted to a harvest (weight) differential, then the difference in daily harvest per canoe becomes 0.7 kg. This economically derived result was not significantly different ($P>0.10$) from the value of 0.8 kg directly measured through the CAS. Thus, information from the SES and CAS corroborated one another and showed that, for the system under study, estimates of fishing success could be used to make inferences about the profitability of fishing as a household enterprise. In the present case, a seemingly small daily difference in fishing success implied an annual difference in net profit of 63,440 CFA ($160). This amount represented roughly 3 months of minimum wage at official GON rates in effect over the period of study.

Management Strategy

It is our intent here to emphasize key considerations relative to development of a management strategy for the Niger River fishery in Niger. Critical points from the discussion thus far are:

1) Fishing pressure, both in terms of the number of canoes and the kinds of fishing gear in use, has had a measurable effect on the abundance and sizes of commercially harvested species, particularly in the southern part of the river.
2) The effects of fishing on surplus production are not constant, but vary with environmental conditions. In the present case, the particular environmental stress was the severe low flow regime caused by the drought.
3) Fishing was the primary source of household income (82 %) and this amount was generated primarily by sale of the larger, more commercially valuable species.
4) A meaningful portion of the harvest (20 %) entered the households for direct consumption by family members.
5) The fishery has shifted from one dominated by migratory fishermen to one primarily composed of local fishermen.

These points dictate that an effective management strategy must:

1) Control fishing effort;
2) Be capable of modification in response to changing environmental conditions and variable regional situations;
3) Protect the larger, commercially valuable species;
4) Not curtail the flow of fish to households for consumption; and
5) Involve local fishermen, although policies concerning migratory fishermen should not be ignored.

The protection of larger fish cannot be achieved without placing limitations on the kinds of gears used for harvest and possibly also on when and where those gears can be used. Given that overfishing in rivers is most likely to occur under harsh environmental conditions, maximum protective measures would be warrented under low flow periods, but could be relaxed during a series of normal flow years. Cast nets can be overly effective during low water when fish are concentrated and vulnerable. This gear should be totally prohibited during low flow periods, but would be acceptable during normal flow years when effectiveness is reduced. Gill nets should be of a large enough mesh size to protect the spawning stock of commercially valued species. Thus ideally, based on the L30 values from Table 2 and the fish community selection characteristics of the locally mounted gill nets, the minimum mesh size should probably not be less than 50-mm bar mesh.

Sudden implementation of a 50-mm minimum mesh size regulation would be unacceptable economically. It is estimated that about 65 % of the harvest would be lost immediately, though recuperation of the stocks could be rapid, particularly with increased flows. A 40-mm minimum mesh size regulation initially would be more acceptable to the fishermen because harvests would not be as severely reduced. These meshes are still relatively common and thus gear replacement costs would not be prohibitive. The average useful life of a gill net is about 2 yr; allowing fishermen to transition to the new minimum mesh over this period of time would cause less economic hardship. Initiation of the regulation with the re-occurrence of higher flows and increased production would further lessen negative effects on fishing families. If a 40-mm minimum mesh was to be successfully implemented, than a further increase to 50-mm could be attempted later if continued monitoring of the fishery showed it to be necessary.

In an effort to maintain the flow of fish to the households, it would be reasonable to allow women and children to use "noncommercial" gear, e.g., small hand traps, nets, and hooklines, in shoreline areas. It is assumed that this kind of fishing pressure would not be detrimental to the stocks of commercially valuable species, though immature individuals of these species will surely be captured. It is certainly feasible that household members engaging in this kind of fishing can be taught, and already are able to some degree, to recognize small individuals of valuable species which could then be culled, allowing the smaller species to make up the major part of the fish going directly into the households for consumption.

In most developing countries in Africa, government fisheries agencies exist in a rudimentary form and their main purpose is to enforce regulations that, in many cases, are not well founded and are certainly not enforceable. Conflicts between agencies and fishermen can arise and generally there is little cooperation toward developing workable management strategies. Typically, management has been approached in a "westernized" fashion with an emphasis on strong government authority. It has been shown repeatedly that top-down management of these fisheries cannot work in Africa and thus should be abandoned, or minimally, highly modified to minimize dependence on government infrastructure.

Scudder and Conelly (1984) argue that there have been, and still are, traditional management systems based on localized, community-level authorities with responsibilities over river resources. Probably the most in depth description of indigenous management systems on the Niger River is that of Sissoko et al. (1986), the essence of which can be described as follows: In the Central Delta of the Niger River in Mali, the Bozo and Somono fishermen divide the river waters adjacent to their communities into fishing zones called "bamo." Each bamo is opened and closed on specific dates. Some bamo are left opened permanently as a daily source of food for the community. Opening and closing dates are flexible to accommodate unusual situations; for example, most bamo are put in reserve earlier and stay closed longer in years of low water. Management of bamo is in the hands of the village chief, the spiritual leader and the council. They decide which fishing zones will be in reservation, fix the opening and closing dates of the zones, estimate the part of the harvest that should go to the community for public purposes, and provide effective protection. Generally, the reserves are protected by a community watch program; however, the council may select some of its members as guardians. It is in the tradition of the community to respect the rules and violating them is regarded as a crime and an act of dishonor.

In Niger, the current study documented that there are localized, traditional systems for regulation of the fishery and that the fishermen have a desire to organize and to be given responsibility for management of the resource. The fishermen realize that resource deterioration has occurred, want to preserve their vested interests, and presently are forming management organizations. Thus, the development of localized fishery management authorities is not a vague possibility, but a current reality that must be carefully nurtured. These community-level organizations are the only real possibility of implementing management programs with enforcement potential beyond the limited capabilities of the government.

Ideally, the fishermen organizations should be given authority to establish regional regulations concerning protected fishing areas and limited entry into the fishery, directed at both local and migratory fishermen. Government should assist in this restructuring process and provide extension and education programs that will allow the fishermen to make the best decisions with respect to their regional management responsibilities. The following activities should be major fishery agency priorities:

— Gathering and disseminating information needed by fishing communities for planning their management strategies.

— Working with fishermen on the application of new fishing methods or management ideas.

— Monitoring fish resources and other household enterprises under various management practices.

— Helping to enforce strict fishing regulations when warranted and agreed to by all parties involved.

— Enhancing communication between fishing communites and national fishery agencies.

— Contributing to multinational management strategies in the river basin.

On a larger scale, it is certain that if information is not available on the importance of African river fisheries in terms of employment, amount of harvest, market value and socionutritional benefits to families, then the potential is small that fisheries will be taken into account by river basin planning authorities. It is estimated from government of Niger reports that about 20 % of the available floodplain habitat has been isolated for rice production, which roughly implies an equivalent reduction in the carrying capacity of the riverine system (Welcomme 1976). Any mainstream impoundment of the river above Niger would insure that the low flow regime existing today would continue to exist in the future with a concomitant loss of fish production. It is likely that under these conditions, based on the assessment presented earlier, future yields would not exceed 2 500 t per annum in Niger, presupposing that workable protective measures were in place. The need for good biosocioeconomic documentation of riverine fisheries, leading to development of viable management plans, is paramount if rivers are to continue to play a vital role in the well-being of the people of Africa.

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References

Bazigos, G. P.. 1974. Design of fisheries statistical surveys for inland waters. FAO Tech. Pap. No. 133, Rome. 122 p.

Beadle, L. C. 1974. The inland waters of tropical Africa. Longman, New York, NY. 365 p.

Daget, J. 1962. Les poissons du Fouta-Djalon et de la Basse Guinée. Mem. I.F.A.N. 65: 1–207.

Daget, J., and A. Iltis. 1965. Poissons de Côte d'Ivoire (eaux douces et saumâtres). Mem. I.F.A.N. 74: 1–387.

Dobrovici, N. B. 1971. Niger developpement et la rationalisation de la pêche sur le fleuve. Niger — rapport du gouvernement. FAO/UNDP Tech. Assist. Rep. No. TA 2913: 46 p.

Drijver, C. A., and M. Marchand. 1985. Taming the Floods. Environmental aspects of floodplain development in Africa. Center for Environmental Studies, State University of Leiden, Leiden. 197 p.

Scudder, T., and T. Conelly. 1984. Management systems for riverine fisheries. Inst. Dev. Anthro., Binghamton, NY. 87 p.

Shell, E. W. 1986. Tapestry of people, of hunger, and of fishes, p. 48–64. *In* S. T. Younkin [ed.] Proceedings of the Philadelphia Society for Promoting Agriculture 1985–86. The Philadelphia Society for Promoting Agriculture, Philadelphia, PA. 68 p.

Sheves, G. 1981. Etablissement de centres communautaires de peche artisanale au Niger, analyse économique. FAO/UNDP Document de Travail No. 4: 37 p.

Sissoko, M. M., S. P. Malvestuto, G. M. Sullivan, and E. K. Meredith. 1986. Inland fisheries in developing countries: an opportunity for a farming systems approach to research and management, p. 297–317. *In* C. B. Flora and M. Tomecek [ed.] Selected Proceedings Farming Systems Research Symposium, Kansas State University Office of International Agricultural Programs, Manhatten, KS. 584 p.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

Welcomme, R. L. 1976. Some general and theoretical considerations on the fish yields of African rivers. J. Fish Biol. 8: 351–364.

1978. Some factors affecting the catch of tropical river fisheries, p. 266–277. *In* R. L. Welcomme [ed.] Symposium of River and Floodplain Fisheries in Africa. CIFA Tech. Pap. No. 5. FAO, Rome. 378 p.

1979. Fisheries ecology of floodplain rivers. Longman, New York, NY. 317 p.

1985. River fisheries. FAO Tech. Pap. 262: 330 p.

Environmental Impact of Ganga Basin Development on Gene-Pool and Fisheries of the Ganga River System

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NATARAJAN, A.V. 1989. Environmental impact of Ganga Basin development on gene-pool and fisheries of the Ganga River system, p. 545–560. *In* D. P. Dodge [ed] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Abstract

Much of the ecological malady that afflicts the Ganga River system and the recent decline in its fisheries are traceable to the impacts of cultural development associated with population growth in the Ganga Basin. Among these, irrigation projects and flood control measures have nearly destroyed floodplains, sloughs, inundation zones, and oxbow lakes, all of which are breeding habitats of the major carps. The impairment of recruitment in these fish has set into motion changes and readjustments of fish populations at the second and third trophic levels. The major carp populations, *Labeo rohita* (Ham.), *Cirrhina mrigala* (Ham.), and *Catla catla* (Ham.) are now declining, while minor carps and other less economic species are increasing in relative abundance. The impact of irrigation projects on fisheries is compounded by land use practices, pollution, exploitation, and fishing. Hydraulic structures have all but eliminated the fishery for anadromous *Hilsa ilisha* (Ham.) in riverine stretches of the Ganga River. The present paper emphasizes rehabilitation and the use of management techniques to protect the diminishing gene-stocks and to augment fisheries of the Ganga River system. Such management conforms to a holistic approach which places fisheries in the perspective of the total environment.

Résumé

NATARAJAN, A. V. 1989. Environmental impact of Ganga Basin development on gene-pool and fisheries of the Ganga River System, p. 545–560. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium, Can. Spec. Publ. Fish. Aquat. Sci. 106.

Une bonne partie de la dégradation écologique qui affilige le réseau hydrographique du Gange et la baisse récente de la pêche qu'on y pratique sont attribuables aux répercussions du développement cultural lié à la croissance démographique dans le bassin du Gange. Entre autres, les projets d'irrigation et les mesures de lutte contre les inondations ont presque détruit les plaines inondables, les marécages, les zones d'inondation et les lacs en croissant, qui sont tous des habitats de reproduction pour les principales espèces de carpe. La diminution du recrutement chez ces poissons a déclenché des changements et des rajustements des populations de poisson aux deuxième et troisième niveaux trophiques. Les principales populations de carpe, *Labeo rohita* (Ham.), *Cirrhina mrigala* (Ham.) et *Catla catla* (Ham.) connaissent actuellement une baisse, tandis que l'abondance relative des espèces mineures de carpe et d'autres espèces moins importantes sur le plan économique s'accroît. Les répercussions des projets d'irrigation sur les pêches s'ajoutent aux problèmes engendrés par les méthodes d'utilisation des terres, la pollution, l'exploitation et la pêche. Des structures hydrauliques ont presque éliminé la pêche de l'espèce anadrome *Hilsa ilisha* (Ham.), dans les sections fluviales du Gange. Le présent article met l'accent sur la remise en état et l'utilisation de techniques de gestion visant à protéger les effectifs de gène qui diminuent et à accroître les ressources halieutiques dans le réseau hydrographique du Gange. Cette gestion est conforme à une approche holistique qui place les pêches dans la perspective de l'environnement global.

Introduction

The Ganga River is the most important river system in India and one of the largest in the world. The river system covers upland stream, warmwater, swampy, and deltaic habitats. The rich ichthyofauna of 141 species includes major carps, large catfishes, mahseers, and the anadromous hilsa. The river has provided a major source of freshwater fisheries since earliest settlement of the area. The basin has undergone an accelerated rate of development following demographic growth during the past three and a half decades. Irrigation and hydroelectric projects, flood control measures, urbanization and industrialization, modernization of agriculture and changes in land-use patterns during this period have resulted in large-scale changes in the river regime and in the morphometry of the river bed, floodplains, and oxbow lakes, causing degradation of water quality. The ecological impact of these changes, coupled with sustained massive destruction of broodstrock, fry and fingerlings and unregulated fishing effort, has been reflected in a diminished fishery with distinct changes in structure. Many fish stocks face possible extinction.

Developing countries view rivers as an important source of food fish and as a source of employment for large numbers of people who live on the river banks and depend on the fishery for their livelihood. This situation is especially true of the Ganga River, where the sustained fishery provides employment during much of the year to well over 24 000 fishermen (who support four times as many dependents).

The multiple use of resources, including water, is a well-accepted principle to achieve social and economic objectives of development and is inevitable in the face of a growing population. However, while due consideration is given to demands of irrigation, hydroelectric power, navigation, and industry, and while efforts are now underway to improve water quality for public health, drinking and bathing, the interests of the biological resources of the Ganga River have been neglected. This neglect is reflected in the lack of any design for optimal allocation of waters from the Ganga River, and is accentuated by a lack of appropriate systems for rehabilitation and management of fishery resources.

Ganga Basin: Physiography

The Ganga River basin (70° to 88° 30'E longitude and 22° to 31° N latitude) covers an area of about 1×10^6 km^2 and includes part of the territories of India, Nepal, Bangladesh and China. Within India it drains some 861×10^3 km^2 of the states of Haryana, Uttar Pradesh, Bihar, West Bengal, Rajasthan, Madhya Pradesh, Himachal Pradesh, and Delhi and covers more than a quarter of India's total area. The plain is bounded on the north by the Himalayan fold mountains and on the south by the Vindya mountains and the Peninsular shield.

Climate

Daily mean air temperatures rise above 40°C in many places during the hot season (April to June) yet during the cold season (December to February) may fall below 10°C in the western part of the basin. The southwest monsoon breaks in early June at the mouth of the Ganga and reaches the western end of the river system by end of July. The rainy season extends from July to October. Precipitation ranges from <400 mm• yr^{-1} in the western part to 1 600 mm• yr^{-1} in the east and may exceed 2 000 mm• yr^{-1} in the Himalayas. (Das Gupta 1984).

River and River Morphology

The Ganga rises in the Garwal Himalayas (30°55'N, 70°7'E) from the Gangotri glaciers at an altitude of 4 100 m a.s.l. (Fig. 1). The river enters the plains at Rishikesh. Upland reaches distinguished by steep slopes, cascades and waterfalls, have a general slope of 1 in 67 and extend for 250 km in Uttar Pradesh. The Upper Ganga traverses the Ganga plain between Rishikesh and Allahabad in a stretch of 770 km and a slope of 1 in 4 100. The middle Ganga extends from Allahabad to Farakka, 1 005 km long and a slope of 1 in 13 800. This stretch runs through parts of Uttar Pradesh, Bihar, and West Benhal. In Bihar, the river is characterized by meanders, loops, oxbow lakes, and extensive floodplains.

The lower Ganga extends from Farakka to the Bay of Bengal, a stretch of 470 km; the lower half of this stretch was tidal before the construction of Farakka barrage. The slope of this segment of the river is 1 in 24 000. The total length of the main channel of the Ganga is 2 525 km from source to mouth. The principal Himalayan tributaries include the Ram Ganga, Gomti, Ghaghara, Gandak, and Kosi rivers, all with steep gradients. The river breaks into a number of interlaced channels in the Ganga plain with extensive floodplains, meanders, oxbow lakes and swamps in its northern tributaries. In addition, the Kosi River is renowned for changing its course and abandoning channel beds. The Yamuna tributary, which also rises in the Great Himalayas, joins the Ganga River from the south at Allahabad. The Chambal River is a major tributary that rises in the Vindya range and Peninsular plateau to join the Yamuna from the south. The Damodar joins the lower Ganga in Bengal where the river is tidal. These tributaries have a combined length of approximately 10 000 km, the total system is 12 500 km in length.

Hydrography

River waters are derived from rainfall, chiefly from the southwest monsoon, and from glacial melt in summer. The physical features of the drainage basin and the nature of the bedrock also influence the hydrological regime of the Ganga and its tributaries. The main Ganga carries its maximum volume of water during July–September at flow rates between 40 000 and 50 000 m^3• s^{-1}, but the rate dwindles to about 3 000 m^3• s^{-1} in winter and summer months. The mean annual rate of flow in many small tributaries is <400 m^3• s^{-1}. The Ganga receives large annual inflows from its tributaries. The river discharges about 384 billion m^3• yr^{-1} out of a total surface runoff of 469 billion m^3• yr^{-1}.

Petrography and Soil

The Vindya and the Peninsular plateau, which give rise to the southern tributaries and the Damodar, are much older than the Himalayas and are tectonically related to the Indian shield (Rao 1979). The Vindya range consists largely of sedimentary rocks while the Peninsular Plateau is formed of crystalline rocks. The Himalayas generally are crystalline and metamorphic rocks (granites, gneisses and schists in the Great and Middle Himalayas) and sedimentary rocks in the Lower Himalayas which are <1000 m (Sivaliks). The central Himalayas in Nepal, where the Ghaghara, Gandak, and Kosi tributaries rise, are largely composed of metamorphosed limestone. The mountain, submontane, alluvial and red soils, which together form 65 % of the soil types in the Ganga basin (Das Gupta 1984), are susceptible to very high rates of erosion.

Water Extraction

The total length of the canal network in the Ganga basin, now about 9 500 km, is to be extended to 13 680 km (Das Gupta 1984). Eighteen major canal structures on the Ganga River system irrigate about 7 million hectares of agricultural land. Some dams have been erected on northern and southern tributaries, for irrigation, hydro-power generation and flood control. Approximately 33.5 billion m^3 of water are stored in reservoirs in the Ganga basin, and more storage reservoirs are likely. The river system has many weirs/bar-

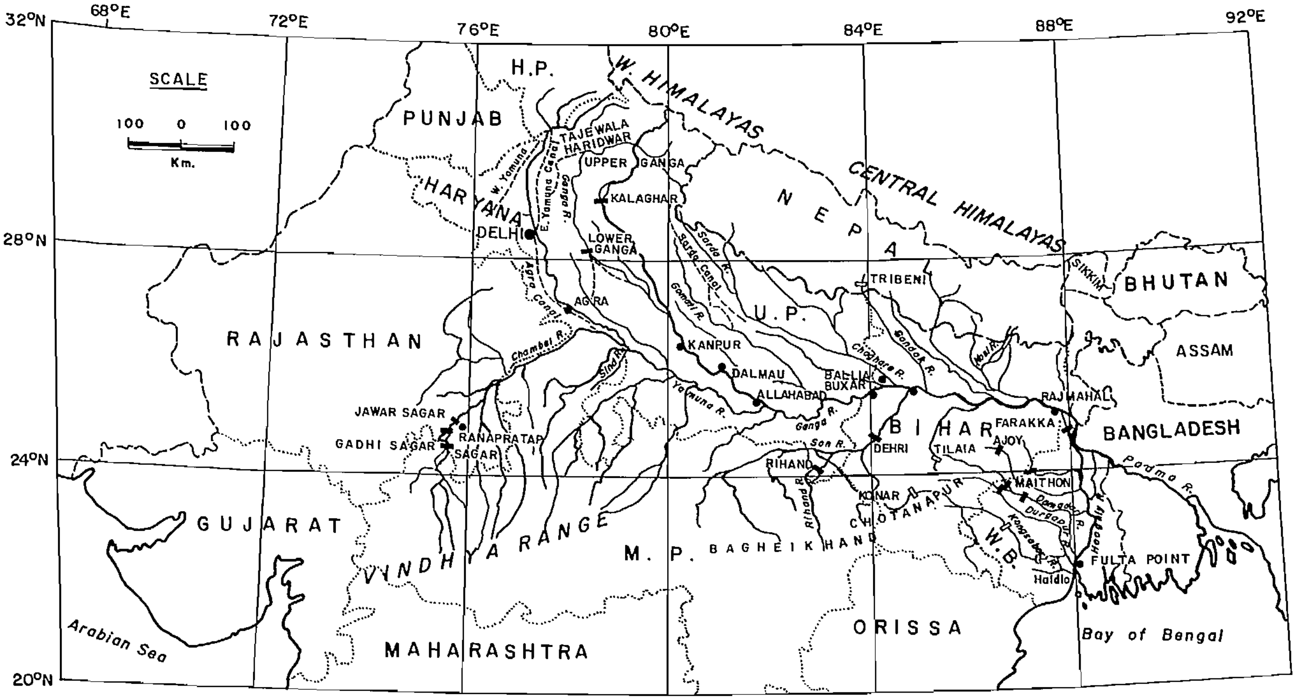

FIG. 1. The main Ganga River and its northern and southern tributaries with major canal projects and storage reservoir locations.

rages, including those at Hardwar, Narora (Upper Ganga), Farakka (lower Ganga), Kota (Chambal), Tajewala, Okhla (Yamuna), Tribeni (Gandak), Hanumannagar (Kosi), Dehri (Son), and Durgapur (Damodar).

Pollution

Industries that contribute significantly to the pollution of the Ganga River system include pulp and paper, textile, tanning, sugar refineries, distilleries, oil refineries, fertilizer, pesticide, chemical, steel, paint and varnish, rubber and jute plants; there are also coal wash sites and thermal power plants (Dalela 1984). Toxic materials include acid and alkaline wastes, heavy metals, free chlorine, iron chlorides, free ammonia, sulphate, oil, grease, organic wastes, phenols, sulphide, cyanide, fly ash, thermal waste, detergents, and pesticides. High levels of zinc, copper and chromium are discharged from viscose rayon plants into the deltaic stretch of Ganga. These materials concentrate in lower trophic levels and fish. Bioaccumulation of heavy metals has been observed in benthic invertebrates and 25 species of fish in the lower Ganga (Ghosh et al. 1982).

Details of the impact of industrial pollution on water quality and aquatic life in the Ganga and Yamuna rivers are in Table 1.

Sewage and industrial organic wastes pose a serious threat to water quality and benthic life and cause deoxygenation of the river. High BOD values in the Ganga River occur around large industrial cities like Kanpur (BOD load 61 $t \cdot d^{-1}$) and Calcutta (BOD load 106 $t \cdot d^{-1}$), the Yamuna around Delhi (BOD load 130 $t \cdot d^{-1}$) and the Damodar around Durgapur-Assansol (BOD load 43 $t \cdot d^{-1}$) (Dalela 1984). The impact is much higher in tributaries with low flow-rates, such as the Son, Gomti, Suvaon, Kali and Daha rivers, where summer fish kills are common. Fly ash and coal particles have also contributed to diminished productivity of macroinvertebrates. Municipal sewage effluent carries domestic and trade wastes containing heavy metals, hydro-carbons, synthetic detergents, etc. Heavy metals like Zn (1.6 $mg \cdot L^{-1}$), Cu (7.5 $mg \cdot L^{-1}$), Fe (115 $mg \cdot L^{-1}$) and Mn (95 $mg \cdot L^{-1}$), have been recorded in Calcutta city sewage (Ray et al. 1981). Synthetic detergents like alkyl benzene sulphonate (ABS) in the range of 0.2–2.0 $mg \cdot L^{-1}$ has been encountered in the sewage water of Delhi, Kanpur and Calcutta. These substances are toxic to fish life and are not bio-degraded easily.

Ichthyofauna

The Ganga River system includes upland streams, extensive warmwater stretches, floodplains, sloughs, oxbow lakes, and backwaters, which present a mix of ecologically distinct habitats that are reflected in the rich range of ichthyofauna. Much information has become available on the ichthyofauna of the country over the past 100 years. Menon (1974) listed 141 species occurring in the Ganga River system belonging to 72 genera, 30 families, and 11 orders (Table 2). There is a wide variety of upland stream fish: 9 species of Rasborinae, 11 species of Cyprinidae, including two species of snow trout, *Schizothorax kumzonensis* (Menon) and *Schizothoraichthys progastus* (McClelland) and two species of mahseers, *Tor putitora* and *Tor tor*; 3 species of Psilorhynchidae; 2 species of Homalopteridae; 13 species of Cobitidae (loaches); and 20 species of Sisoridae. The warmwater lotic species of economic importance are: the major carps *Catla catla*, *Cirrhina mrigala*, *Labeo rohita*, *Labeo calbasu*, and the large catfishes, *Mystus aor*, *M. seenghala*, *Rita rita*, *Wallago attu*, *Silonia silondia*, *Pangasius pangasius* and *Bagarius bagarius*. The featherback *Notopterus chitala* and murrel

TABLE 1. The effect of industrial waste discharge on water quality and aquatic life in the Ganga River system.

River tributary	Location	Discharge volume ($m^3 \cdot d^{-1}$)	Type of discharge	Effects on water/sediment quality	Effects on aquatic life
Ganga	Rishikesh	9×10^3	Chemicals	• No measured effects	• Direct effect on aquatic life not recorded
	Kanpur	167×10^3	Tannery and textile wastes, and mixed organic wastes	• Depletion of DO; a BOD load of 61 $t \cdot d^{-1}$.	• Growth of undesirable fauna
	Allahabad	No data	Fertilizers	• High ph • Ammonia toxicity	• Disappearance of plankton and benthic fauna up to 300 m downstream
	Barauni	No data	Oil-bearing wastes	• No data	• Fish mortality and damage to major and minor carps, catfishes and murrels
	Calcutta	1134×10^3	Industrial wastes containing lignin, heavy metals, pesticides, detergents, etc.	• High BOD load of 106 $t \cdot d^{-1}$ • Low Do • Metals and pesticides in sediments. • Reduction in primary productivity	• Reduction in plankton population. • Absence of benthos around outfalls. • Presence of Zn, Cu, Cr, DDT, BHC in fish and other biota
Yamuna	Delhi	1875×10^3	• Chemicals, DDT factory wastes, oil and grease, heavy metals and detergents	• BOD load of 130 $t \cdot d^{-1}$ • Organic pollution • DDT residue in water (0.6–3.5 ppb) and sediment	• DDT residue in fish and other biota
	Mathura	• No data	• Oil-bearing acidic wastes	•No data	•No data
	Agra	• No data	• Tannery and trade, etc.	• No data	• No data

BOD values include sewage and industrial organic waste load. (Dalela 1984).

Channa marulius also belong to this large species category. Species found in marshy habitats include *Clarius batrachus*, *Heteropneustes fossilis*, *Channa* spp., *Amphipnous cuchia*, *Anabas testudineus*, *Mastacembelus* spp., *Notopterus notopterus*, and *Gadusia chapra* and represent a mixture of families and orders. The anadromous hilsa, *Hilsa ilisha* is of great economic importance. The rest include minor carps, small catfishes, minnows, small clupeids and others. The distribution of species by habitat is in Table 3, excluding exotic carps and salmonids.

Breeding and Migratory Habits of Economically Important Fishes

Major carps of the Ganga breed during the monsoon. Breeding starts earlier in the Bengal basin, where the monsoon extends from April to August (David 1959). In the Kosi River, the early breeding of major carps in May is caused by snow-melt. With the exception of the Gomti, none of the tributaries in the western basin overflow their banks except with exceptionally heavy floods. Spawning is thus delayed as late as August and September in western Uttar Pradesh.

The major carps make migrations of intermediate length during the breeding period and prefer grassy substrates, highlighting the importance of floodplains and similar low-lying habitat. *L. dero* and *L. dyocheilus* seek upland reaches for breeding. The mahseer (*Tor tor* and *T. putitora*) move upstream from the plains and breed in shallow areas over gravelly bottoms in August–September during the low-flow period. Among the large catfishes, *W. attu* breeds at the same time and in a similar habitat as the major carps. However, most catfishes, like *Mystus seenghala*, *M. aor*, *Eutropiichthus vacha*, *Ompok bimaculatus*, and *Ompok pabda* breed between late summer and monsoon period. *Rita rita* and *Clupisoma garua* breed as early as March (Karamchandani and Motwani 1955). Karamchandami and Motwani (1956) report summer breeding for the catfishes *Silonia silondia*, *Ailia coila*, *Ailiichthys punctata* and *Gagata cenia*. *Pangasius pangasius*, which remains in deltaic stretches, seeks freshwater sites for breeding (Day 1889). *B. bagarius* also migrates upstream to reproduce. Qasim and Qayyum (1962) reported a prolonged breeding season (June–October) for *Channa striatus* and *Channa marulius*. The grey mullet *Mugil corsula* and spiny eel *Rhynchobdella aculeata* also breed coincidentally with the rainy season. Swamp fishes prefer marshy habitats and

TABLE 2. Number of orders, families, genera, and species represented in the catch and the fish species encountered in landings in the Ganga River system.

	Class Osteichthyes			
Order	Family	Genera	Species	Species occurring in landings
Clupeiformes	2	3	4	*Hilsa ilisha* (Ham.) *Setipinna phasa* (Ham.) *Gadusia chapra* (Ham.)
Osteoglossiformes	1	1	2	*Notopterus chitala* (Ham.) *Notopterus notopterus* (Pallas)
Cypriniformes	4	27	67	*Catla catla* (Ham.) *Cirrhina mrigala* (Ham.) *Cirrhina reba* (Ham.) *Labeo rohita* (Ham.) *Labeo calbasu* (Ham) *Labeo bata* (Ham.) *Labeo boga* (Ham.) *Labeo gonius* (Ham.) *Labeo dero* (Ham.) *Labeo dyocheilus* (Ham.) *Tor putitora* (Ham.) *Tor tor* (Ham.) *Oxygaster bacaila* (Ham.) *Chela laubuca* (Ham.) *Amblypharyngodon mola* (Ham.) *Aspidoparia morar* (Ham.) *Puntius sarana sarana* (Ham.)
Siluriformes	10	22	41	*Mystus aor* (Ham.) *Mystus seenghala* (Sukes) *Mystus cavasius* (Ham.) *Rita rita* (Ham.) *Ompok bimaculatus* (Bloch) *Ompok pabda* (Ham.) *Wallago attu* (Schneider) *Ailia coila* (Ham.) *Clupisoma garua* (Ham.) *Eutropiichthys vacha* (Ham.) *Silonia silondia* (Ham.) *Pangasius pangasius* (Ham.) *Bagarius bagarius* (Ham.) *Gagata cenia* (Ham.) *Clarias batrachus* (Linnaeus) *Heteropneustes fossilis* (Bloch)
Atheriniformes	2	3	3	
Gasterosteiformes	1	1	1	
Channiformes	1	1	4	*Channa marulius* (Ham.)
Symbranchiformes	1	1	1	
Perciformes	6	10	14	*Rhinomugil corsula* (Ham.) *Glossogobius gutum* (Ham.) *Anabas testudineus* (Bloch)
Mastacembeliformes	1	2	3	*Mastacembelus armatus* (Lacepede) *Mastacembelus pancalus* (Ham.) *Macrognathus aculeatus* (Bloch)
Tetraodontiformes	1	1	1	
	30	72	141	

breed during July–October. *Hilsa ilisha* ascends as far as 1 500 km from the river mouth to Allahabad and is known to move up to Kanpur on the main Ganga and 100 km upstream in the Yamuna River in years of exceptional abundance.

Prawns, *Macrobrachium choprai* (Tiwari) occur in the middle strech of the Ganga, while six other species of *Macrobrachium* remain in the delta, making migrations between non-tidal and tidal reaches. *M. rosenbergii* and *M. malcolmsonii* are economically important (Rajyalakshmi 1980; Kurian and Sebastian 1982).

Physico-Chemical Parameters of the River

The main features of the hydro-chemistry of the upper (Kanpur), middle (Allahabad and Bhagalpur) and lower reaches of the Ganga for 1959–60 and 1980 are in Table 4, based on information from Pahwa and Mehrotra (1966),

TABLE 3. Ecological grouping of fishes and prawns of the Ganga River system.

Species	Species number	Economically important species	Others
Fish			
Hill stream	55	7	51
Swamp	13	7	6
Plain	72	13	36
Anadromous	1	1	—
	141	28	93
Prawns			
Freshwater	1	1	—
Deltaic (Freshwater and tidal)	6	2	4
	7	3	4

Ray and David (1966), Ray et al. (1966), annual reports of the Central Inland Fisheries Research Institute (CIFRI), India (1980, 1981, 1982).

Turbidity has increased in the upper and middle reaches of the Ganga between 1960 and 1980. The water seems to have high buffering capacity, and only limited fluctuations have been noted in pH (7.5–8.5) throughout the entire stretch. Alkalinity and chloride showed a remarkable increase between 1959–60 and 1980 at all places. The increase in alkalinity may be due to qualitative changes in runoff. Heavy sewage discharge from urban settlements and cities may be responsible for increases in chloride content. Nutrient levels have shown a tendency to increase in some places. Silicate has increased significantly. Away from sites of high BOD loading, DO levels are largely unchanged.

Following the construction of a barrage at Farakka in 1975 and the subsequent regulated discharge, the lower Ganga showed a significant change in salinity. Before the barrage was installed the tidal reach extended up to Nabadwip (0.2‰ salinity). After construction of the barrage the tidal reach receded and freshwater now extends to Diamond Harbour, a distance of 150 km downstream of Nabadwip. Before 1975, the average value for surface salinity at Diamond Harbour was 12.0‰ but since 1975 it has dropped to 0.118‰. Silicate has increased considerably in this extended freshwater zone.

Primary Production

Using information at Bhagalpur (middle Ganga) and Nabadwip (lower Ganga), estimates indicated that primary producers fixed only 0.274 to 0.307 % of the available light energy (CIFRI 1980, 1981, 1982) and Kimbal (1935) (Table 5).

Biotic Communities

Plankton

Changes in plankton abundance and community structure over a 20-yr period are based on observations by Shetty et al. (1961) and Pahwa and Mehrotra (1966), and material reported in annual reports of CIFRI (1980, 1981, 1982). Diatoms, represented by *Synedra* spp. and *Fragilaria* spp., dominated river stretches at Kanpur and Allahabad; Chlorophyceae, represented by *Mougeotia*, *Spirogyra*, *Pediastrum* were dominant at Bhagalpur. Rotifers (*Brachionus* and *Keratella*) and copepods (*Cyclops* and *Diaptomas*) dominated the zooplankton population throughout the year. Studies at Bhagalpur showed an appreciable increase in the plankton counts in 1980 (1 247• L^{-1}) in relation to 1960 values (610• L^{-1}). In 1980, Chlorophyceae were the dominant phytoplankters, and rotifers and copepods were the dominant zooplankters. The composition of plankton has not changed much since 1960 but abundance has increased significantly in upper and middle reaches of the Ganga.

TABLE 4. Physico-chemical parameters of the Ganga River.[a]

Centres	Kanpur		Allahabad		Bhagalpur		Nabadwip to Calcutta	Calcutta to Diamond Harbour	Pre-Farakka barrage Nabadwip to Diamond Harbour
Year	1959	1980	1959	1980	1960	1980	1980	1980	1953–54
Water temperature (°C)	16.0-32.3	—	17.5-31.5	17.5-32.5	18.5-31.5	18.0-30.0	17.5-32.0	18.5-33.5	19.8-32.8
Turbidity (JTU)	<100-1283	—	<100-1170	157-1650	<100-1230	<120-1400	<100-71 000	<100-71 000	—
DO (mg• L^{-1})	4.2-8.0	4.35-8.2	4.9-10.4	4.0-10.0	5.2-0.1	4.5-8.18	5.0-10.8	5.0-10.8	3.4-5.1
pH	7.6-8.3	—	7.7-8.3	7.8-8.2	7.5-8.2	7.6-8.5	7.6-8.5	7.8-8.5	7.9-8.4
Alkalinity (mg• L^{-1})	80-196	—	109-251	210-410	86-187	130.35-212.0	68-195	72.0-180	102-357
Cl (mg• L^{-1})	4.0-16.0	15.7-21.7	4.0-20.2	18.0-30.0	5.0-17.2	26.16-75.15	—	—	—
Salinity ‰	—	—	—	—	—	—	Traces	0.118	0.2-12
NO_3 (mg• L^{-1})	0.113-0.22	—	Traces-0.2	0.06-0.48	0.06-0.17	0.01-0.28	Traces-0.224	Traces-0.27	0.03-0.11
PO_4 (mg• L^{-1})	0.067-0.21	—	0.03-0.21	0.08-0.45	0.06-0.12	0.012-0.18	Traces-0.61	Traces-0.31	0.066-0.142
Specific conductance (umhos• cm^{-1})	—	—	—	—	—	324-548	143-479	199-799	—
SiO_3 (mg• L^{-1})	8.2-20.3	—	6.7-17.0	18.0-20.0	3.5-12.3	2.5-20.4	3-27	1-25	2.7-9.1

[a] Source: data from literature cited in the text.

TABLE 5. Estimated production potential of the Ganga River at Bhagalpur (middle Ganga) and Nabadwip (lower Ganga) for the years 1980–82. (Central Inland Fisheries Research Institute (CIFRI), Barrackpore, Annual Reports 1980, 1981, 1982.)

Centres	Energy fixed by primary producers				Fish	
	Visible light energy on the water surface (cal•m^{-2}•d^{-1})	Gross (cal•m^{-2}•d^{-1})	Net (cal•m^{-2}•d^{-1})	Photosynthetic efficency %	Potential yield (kg•ha^{-1}•yr^{-1})	Actual yield (kg•ha^{-1}•yr^{-1})
Bhagalpur (Middle Ganga)	1 870 000	5 124	2 651	0.274	93.1	25.9
Nabadwip (Lower Ganga freshwater zone)	1 960 000	6 017	2 981	0.307	104.7	10.4

In the lower Ganga both plankton composition and abundance showed remarkable changes after the construction of the Farakka barrage. Plankton counts ranged from 37 to 95• L^{-1} during the pre-barrage years, but increased to 145 to 304• L^{-1} in the post-barrage year 1980. During 1960, estuarine forms such as the phytoplankton *Coscinodiscus cranii*, *Asterionella sapponica*, *Chaetoceros* spp., and zooplankton *Pseudodiaptomus* sp. *Microsetella* dominated the tidal stretch from Calcutta to Diamond Harbour. After barrage construction freshwater forms became abundant as far downstream as Diamond Harbour. In this area Chlorophycaea has increased by an order of magnitude between 1960 and 1980.

Benthos

In the reach from Kanpur to Bhagalpur benthos declined in abundance (Pahwa and Mehrotra 1966). Insects were dominant at Kanpur and Allahabad, but at Bhagalpur gastropods and bivalves were more common. The average abundance of benthos was as high as 3 476• m^{-2} (insects 3 405• m^{-2}) at Kanpur but decreased to 218• m^{-2} at Bhagalpur (molluscs 124• m^{-2}). Recent studies in the lower Ganga (CIFRI 1985) showed a sharp decline in abundance of benthos (3 to 164• m^{-2}), which may be attributed to paper, pulp and sewage sludge. Maximum numbers (94–164• m^{-2}) were noted at Nabadwip while minima (3–15• m^{-2}) were recorded at Diamond Harbour. Gastropods represented by *Pleurocera* and *Lymnaea* were dominant in Nabadwip while crustaceans, such as *Gammarus*, were dominant in Diamond Harbour.

Energy flow

Energy flows through four trophic levels in the lotic segment of the Ganga ecosystem with primary producers (phytoplankton) forming the first level. The major carps are primary and secondary consumers (second and third trophic levels) (Natarajan 1976, 1979; Natarajan et al. 1975). Catfishes belong to secondary and tertiary consumers (third and fourth trophic levels). Hilsa occupies the third trophic level. These fish show considerable flexibility in feeding and adapt equally to the grazing-based pathways dominant in lotic systems (river and tributaries) and the detritus-based pathways dominant in lentic subsystems (oxbow lakes) of the Ganga (Pathak et al. 1985). In addition, air-breathing catfishes and murrels that occur in degraded oxbow lakes and marshy habitats are secondary and tertiary consumers. Minor carps and minnows share the same trophic level as major carps, minor catfishes share the same trophic levels as large catfishes, and small clupeid species share the same levels as hilsa (Natarajan et al. 1975; Natarajan 1976).

Fishing Effort and Relative Fishing Effort Density

Fishing gear consists of drag nets, gillnets, scoop nets, cast nets, longlines and traps (Hornel 1924).

Drag Nets

The large drag net, known locally as Mahajal, has a total length varying from 500 to 4 000 m, a depth of 3.5–5 m and is operated by 15–30 men using two boats. The net made from a number of pieces of hemp or cotton has head and foot ropes with or without sinkers and a mesh of 5–12 cm bar. Ten variants of this net are used largely for major carps, large catfishes and hilsa. Some shallow nets (1 m) are used for *Mystus aor* and *M. seenghala* while others with smaller mesh sizes (1.5–3.5 cm) are used for minor catfishes, and minor carps. They may or may not have pockets. A small drag net which varies from 9 to 16 m in length, is 3–4 m in depth, has a mesh of 2–6 cm bar, and is used by two men to catch carp and smaller fishes. The net has head and foot ropes, but it is without floats and sinkers. There are three variants.

Drift Nets

Large drifting gillnets vary in length from 240 to 360 m, and in depth from 2.5 to 3 m. Made of 10 pieces of hemp net with head and foot ropes and a mesh of 10–30 cm bar, they are used for large catfishes and major carps. Other types use nylon or cotton with or without foot ropes and sinkers, and with varying mesh bar. Altogether there are 11 types of gillnets used in the Ganga and Yamuna rivers.

Barrier and Purse Nets

Set barrier nets made of hemp, cotton or coconut fibres are used extensively to trap migrating major carps during the early freshets of the monsoon (Wishard 1974) in tributaries of the Yamuna River. The purse net is used chiefly for anadromous hilsa in the middle and lower Ganga and for other fishes in the upper Ganga. The net mouth is framed by two bamboo rods (3–6 m long) corresponding to the upper and lower lips, and these are manipulated by strings to hold the mouth open or closed. This net has a mesh of 5-18 cm bar and is made of cotton.

A village-based fishing gear and craft survey between Agra and Allahabad on the Yamuna and between Bulandsahar and Farakka on the main Ganga River was made by CIFRI during 1957 to estimate total production on sampled catch per unit effort (CIFRI Report 1976, Unpubl. data). However, the diversity of the fishing gear, area or season of operation, and the multiplicity and seasonal occurrence of species made catch per unit effort unsuitable as an index of population abundance. Furthermore, as calibration of effort was not possible under these circumstances, assessment of total catch from catch per unit effort and total effort based on inventory was excluded. Despite these problems, the inventory provided a general measure of relative fishing effort and its impact on fisheries in the Ganga and Yamuna.

Fishing effort in the Ganga is many times higher than in the Yamuna: use of drag nets is six times higher, purse seine net use is three times higher, and there are five times as many craft (Table 6). Purse nets are specific to hilsa which is a major seasonal fishery in the Ganga during July-October; however, this fishery is inconsequential in the Yamuna.

TABLE 6. Fishing villages and fishing effort on main river (Ganga) and tributary (Yamuna) (Based on inventory in 1957). (CIFRI Report 1976; unpubl. data).

River stretch	No.• km^{-1}
Fishing villages	
Yamuna (365 km) Agra to Allahabad)	1.56
Ganga (1000 km) (Allahabad to Farakka)	0.94
Fishermen	
Yamuna	8.67
Ganga	22.35
Fishing effort ratio (Ganga: Yamuna)	2.6:1
Dominant Gear	
Drag net	
Yamuna	17.54
Ganga	104.51
Fishing effort ratio	6:1
Gill net	
Yamuna	2.69
Ganga	2.65
Fishing effort ratio	1:1
Purse net	
Yamuna	2.47
Ganga	7.77
Fishing effort ratio	3:1
Vessel	
Yamuna	1.56
Ganga	7.76
Fishing effort ratio	5:1

Estimation of Catch and Catch Structure

The marketable surplus of fish from each reach of the river is brought to nearby unban centres on the river. These centres formed sampling centres for estimating marketable surplus of catch and also catch structure. There are 22 assembly centres (5 being major centres) on the Ganga and four (2 being major centres) on the Yamuna. The discussion in this paper is largely based on data from two major sampling centres on the Ganga and one major centre on the Yamuna, using catch statistics and catch structure descriptions covering 22 years. Mean catch rates for six year-groups from the Yamuna and the Ganga are in Tables 7 and 8; the catch structure for two year-groups is in Table 9. The assembly centres at Allahabad, Buxar and Bhagalpur are considered representative of middle reaches of the Ganga and the lower segment of the Yamuna, the major fishing zones on the system. The monthly sample period varied between a week and 15 days. The species are from four groups: major carps (*L. rohita*, *C. mrigala*, *C. catla* and *L. calbasu*), large catfishes (*M. aor*, *M. seenghala* and *W. attu*), miscellaneous, including minor carps, carp minnows, minor catfishes, a few large catfishes of rare occurrence, small clupeids, etc., and hilsa (treated as a separate category).

Yield and Yield Rate: Trends between 1958 and 1984

Based on energy calculations (Odum 1957) the potential fish yield comes to 93.1 kg• ha^{-1}• yr^{-1} in the middle Ganga (Bhagalpur) and 104.7 kg• ha^{-1}• yr^{-1} in the lower Ganga (Nabadwip). The actual fish yield from the Ganga River during 1980-82 was 25.9 kg• ha^{-1}• yr^{-1} at Bhagalpur and 10.40 kg• ha^{-1}• yr^{-1} at Nabadwip. Thus it seems that the fish yield from these stretches during 1980-82 were only 9.9-27% of potential yield.

There are no indications that the intensity of fishing in middle reaches of the Ganga and in the lower segment of the Yamuna changed significantly between 1957 and 1981-82. The catch rate is presumed to reflect the abundance of the fish stock.

In the Allahabad stretch of the Yamuna, the catch rate for major carps (in kg• ha^{-1}• yr^{-1}) decreased from 4.19 to 2.02, for catfishes from 2.10 to 1.58, and for hilsa from 0.91 to 0.04, but the catch rate for the miscellaneous group increased from 2.17 to 3.16 between the periods of 1958-69 and 1973-84 (Table 7). By species, *C. mrigala* decreased in annual yield by 71.64%; *C. catla* by 69.45% and *L. rohita* by 68.14% between the periods of 1958-66 and 1974-84. For the same period, large catfishes, (*M. aor* and *M. seenghala*) decreased by 24.73%; *W. attu* by 60.12%; *H. ilisha* by 95.73%, while the yield of *L. calbasu* increased by 157.88% and other miscellaneous fish increased by 51.66% (Table 9).

In the Buxar stretch of the Ganga, the catch rate was very poor for major carps during 1958-84 (less than 1.0 kg• ha^{-1}• yr^{-1}). The catch of large catfishes decreased from 1.31 to 1.09 kg• ha^{-1}• yr^{-1}, and the miscellaneous group from 6.25 to 1.83 kg• ha^{-1}• yr^{-1} between the periods of 1958-69 and 1973-84. This stretch is well known for hilsa (Jhingran 1956), but the catch of this species decreased sharply from 9.28 to 0.08 kg• ha^{-1}• yr^{-1} over the same period (Table 8). The yield of large catfishes, *Mystus* spp. decreased by 38.89%, *W. attu* by 46.06% and *H. ilisha* by 99.07% (Table 9) from 1958-66 to 1977-84.

TABLE 7. Estimated mean annual landings (metric tonnes) of species-groups and yields (kg• ha^{-1}• yr^{-1}) of the tributary Yamuna at Allahabad for the period 1958–84. Source: data from literature cited in the text.

Year	58–59 to 61–62[a]		62–63 to 65–66		66–67 to 68–69		73–74 to 76–77		77–78 to 80–81		81–82 to 85–86	
Species group	Average landing	%	Average landing	%	Average landing	%	Average landing	%	Average landing	%	Average landing	%
Major carps	76.88	41.4	108.45	47.0	87.83	45.1	35.87	32.2	36.32	24.6	49.13	30.0
	(3.53)		(4.99)		(0.04)		(1.65)		(1.67)		(2.76)	
Catfishes	44.45	23.9	49.20	21.3	42.87	22.0	25.69	23.0	32.18	21.8	34.59	21.2
	(2.045)		(2.27)		(1.97)		(1.18)		(1.98)		(1.59)	
Hilsa	14.12	7.6	26.17	11.3	19.40	10.0	1.16	1.0	1.13	0.8	0.34	0.2
	(0.65)		(1.20)		(0.89)		(0.055)		(0.05)		(0.015)	
Miscellaneous	50.28	27.1	46.78	20.3	44.67	22.9	48.76	43.7	78.15	52.9	79.44	48.6
	(2.319)		(2.15)		(2.05)		(2.25)		(3.59)		(3.65)	
Total:	185.73		230.60		194.77		111.48		147.78		163.50	
	(8.54)		(10.61)		(8.95)		(5.13)		(6.80)		(7.52)	

[a] Annual landings estimated from e.g. April 1958 - March 1959.
Figures in parentheses indicate yield in kg• ha^{-1}• yr.$^{-1}$
River stretch covered for fishing: 200 km.
Average width of river: $\frac{\text{(Flood level + Summer level)}}{2}$: 1087 m.
Area based on average width: 21 740 ha.

TABLE 8. Estimated mean annual landings (metric tonnes) of species groups and yield (kg• ha^{-1}• yr^{-1}) of the main Ganga at Buxar and Bhagalpur for the period 1958–84. Source: data from literature cited in the text.

Year	58–59 to 61–62		62–63 to 65–66		66–67 to 68–69		73–74 to 76–77		77–78 to 80–81		81–82 to 83–84	
Species group	Average landing	%	Average landing	%	Average landing	%	Average landing	%	Average landing	%	Average landing	%
Sampling centre: Buxar												
Major carps	7.67	8.4	1.90	4.7	1.40	1.8	3.64	28.6	2.06	14.3	3.41	19.3
	(1.94)[a]		(0.48)		(0.36)		(0.92)		(0.52)		(0.86)	
Catfishes	9.33	10.2	3.93	9.8	2.23	2.8	4.47	35.1	3.84	26.6	4.72	26.7
	(2.36)		(1.00)		(0.56)		(1.12)		(0.96)		(1.20)	
Hilsa	27.7	30.3	17.40	43.4	65.13	82.0	0.56	4.4	0.17	1.2	0.26	1.5
	(7.00)		(4.40)		(16.44)		(0.14)		(0.04)		(0.06)	
Miscellaneous	46.83	51.2	16.87	42.1	10.63	13.4	4.07	31.9	8.36	57.9	9.31	52.6
	(11.82)		(4.26)		(2.68)		(1.02)		(2.12)		(2.36)	
Total:	91.53		40.10		79.30		12.74		14.43		17.70	
	(23.12)		(10.14)		(20.04)		(3.20)		(3.64)		(4.48)	
Sampling centre: Bhagalpur												
Major carps	9.60	12.5	17.62	20.3	24.67	21.4	9.18	12.5	12.68	13.0	7.74	6.8
	(2.19)		(4.02)		(5.63)		(2.10)		(2.89)		(1.77)	
Catfishes	20.15	26.2	19.48	22.4	18.40	16.0	20.23	27.6	27.62	28.3	28.63	25.3
	(4.60)		(4.45)		(4.20)		(4.62)		(6.31)		(6.54)	
Hilsa	4.08	5.3	2.65	3.1	6.0	5.2	0.38	0.5	0.69	0.7	1.78	1.6
	(0.93)		(0.61)		(1.37)		(0.09)		(0.16)		(0.41)	
Miscellaneous	43.18	56.1	47.10	54.2	65.97	57.4	43.58	59.4	56.64	58.0	75.22	66.4
	(9.86)		(10.75)		(15.06)		(9.95)		(12.93)		(17.17)	
Total:	77.01		86.85		115.04		73.37		97.63		113.37	
	(17.58)		(19.83)		(26.26)		(16.76)		(22.29)		(25.89)	

[a] Figures in parentheses indicate yield in kg• ha^{-1}• yr^{-1}
Annual landings estimated yearly from April to March.

Sampling centres:	Buxar	Bhagalpur
River stretch covered for fishing (km):	50	100
Average width of the river (m) = $\frac{\text{Flood level + Summer level}}{2}$:	792	438
Area based on average width (ha):	3960	4380

TABLE 9. Estimated mean annual landings (metric tonnes) of economic species at three sampling centres on the Ganga River and tributary Yamuna (1958-66 and 1977-84.) I = % increase; D = % decrease; Yr = March-April. Source: data from literature cited in the text and unpubl. data of CIFRI.

		Yamuna River			Main Ganga River					
		Allahabad (200 km)			Buxar (50 km)			Bhagalpur (100 km)		
	Species	1958-66	1977-84	% I/D	1958-66	1977-84	% I/D	1958-66	1977-84	% I/D
A	Major carps									
	C. mrigala	36.0	10.21	71.64 D	1.01	0.48	52.47 D	5.30	2.20	58.49 D
	C. catla	16.86	5.15	69.45 D	1.80	0.46	74.44 D	4.99	4.40	11.82 D
	L. rohita	16.67	5.31	68.14 D	1.87	0.79	57.75 D	3.29	2.51	23.71 D
	L. calbasu	9.57	24.68	157.88 I	0.10	0.74	640.00 I	0.25	0.54	116.00 D
	Total (A)	79.11	45.35	42.67 D	4.78	2.47	48.33 D	13.83	9.65	30.22 D
B	Catfishes									
	M. aor & *M. seenghala*	34.28	25.80	24.73 D	4.88	3.11	36.27 D	6.59	11.26	70.86 I
	W. attu	12.54	5.00	60.12 D	1.78	0.96	46.06 D	13.22	17.97	35.93 I
	Total (B)	46.82	30.80	34.21 D	6.66	4.07	38.89 D	19.81	29.23	47.55 I
C	*H. ilisha*	20.16	0.86	95.73 D	22.56	0.21	99.07 D	3.36	0.98	70.83 D
D	Miscellaneous	49.65	75.30	51.66 I	25.17	8.05	68.01 D	45.13	59.24	31.26 D
Total (A+B+C+D):		195.74	152.31	22.18 D	59.17	14.80	74.98 D	82.13	99.10	20.66 I

On the Ganga River at Bhagalpur, the catch rate of major carps decreased from 3.95 to 2.25 kg• ha^{-1}• yr^{-1}; the catch rate for catfishes increased from 4.42 to 5.82 kg• ha^{-1}• yr^{-1} and for miscellaneous fishes rates increased from 11.89 to 13.35 between 1958-69 and 1973-84. The yield of hilsa dwindled to an insignificant level over the same period (Table 8). *C. mrigala* declined in yield by 58.49 %, *C. catla* by 11.82 % and *L. rohita* by 23.71 %. Among large catfishes, *Mystus* spp. increased by just over 70 % and the miscellaneous group by 31.26 % between 1958-66 and 1977-84 (Table 9).

Age, Age-Structure, and Annual Mean Length of Major Carps

The structure of the fishery has changed over the years with a reduction in the number of age-groups in recent years. Length-at-age of various age-groups of Ganga major carps have been described previously (Jhingran 1959; Natarajan and Jhingran 1963; Kamal 1969; Gupta and Jhingran 1974; Khan and Jhingran 1975). Ages were derived from the scale annuli or the Peterson method. Details of length-at-age of major carps are shown for the years 1958-67 in Table 10. The mean annual lengths of major carps in the Yamuna River are given in Table 11 for the years 1967 and 1976-83.

Analysis of age-groups in the major carp fishery between 1976 and 1983 revealed the fishery consisted largely of age-group II for *C. mrigala*, II and III for *C. catla*, III for *L. rohita* and III and IV for *L. calbasu*. The major carp fishery of an earlier period (1958-67) included fish from a larger number of age-groups (I to VIII) for these same species. The fishery between 1958 and 1967 was dominated by young-of-the-year and first year group (≥ 50 % in the catch) (Natarajan and Jhingran 1963; Kamal 1969). This dominance explains the lower annual mean length of major carps in 1967. On the other hand, the upward shift in annual mean length of major carps between 1976 and 1983 is marked by age-groups ≥ II in spite of a reduction in the range of age-groups in the fishery.

Discussion

The foregoing examination of data covering a period of about 25 years suggests that the Channel Section part of the Ganga River system may have a fish production potential of about 100 kg• ha^{-1}• yr^{-1}, but the actual yields are only about 18.5 % (10-27 %). Fish productivity would be much higher if total carbon inflow was considered. Nutrient conditions have remained good, with phosphate levels at 0.12 to 0.61 mg• L^{-1}. Plankton abundance has risen, but the benthic community has diminished in abundance and diversity. Fish production has decraesed by 22 % at Allahabad and by 75 % at Buxar. The increase by about 20 % at Bhagalpur is related to miscellaneous uneconomic species and catfishes entering the catch.

The structure of the fishery has changed drastically, with high-value major carps and hilsa giving place to low-value

TABLE 10. Length (mm) at age of Gangetic major carps species between 1958 and 1967 (based on literature cited in the text).

	Age-group									
Species	I	II	III	IV	V	VI	VII	VIII	IX	X
L. rohita	310	500	650	740	800	850	890	920	940	960
L. calbasu	155	290	390	460	545	615	680	740		
C. catla	295	514	716	923	917					
C. mrigala	268	458	644	736	816	867	924	958		

TABLE 11. Annual mean length (mm) of major carps in the commercial fishery of the Yamuna River at Allahabad for 1967 and 1976–83. (R. A. Gupta, CIFRI Unpubl. data)

	1967	1976–83
C. mrigala	483	508
C. catla	595	617
L. rohita	567	668
L. calbasu	403	438

species. Fishing effort has not increased from the 1957 level; indeed the 1982–83 survey at Allahabad (Gupta, CIFRI, Barrackpore, unpubl. data) shows it has declined. The 1957 level of fishing effort was many times higher in the Ganga than in the Yamuna River and yields per unit length of river were nearly the same in both rivers: 0.77 $t \cdot km^{-1} \cdot yr^{-1}$ (Ganga) and 0.75 $t \cdot km^{-1} \cdot yr^{-1}$ (Yamuna). The high fishing effort depressed the fishery in the Buxar stretch of the Ganga. In addition, many major carp species now face the threat of progressive elimination. The anadromous hilsa, formerly a significant fishery in the Ganga system, has been all but eliminated from middle reaches. The estimated fish production of the Ganga from Allahabad to Farakka (about 1 000 km) is only 770 $t \cdot yr^{-1}$ while for the lower segment of the Yamuna, from Agra to Allahabad (about 365 km) it is some 275 $t \cdot yr^{-1}$. Thus, the problem of fishery management has become extremely complex. Conventional approaches to stock management (unispecies and multi-species models) are no longer appropriate when the fisheries are so disrupted and the production system is starved of recruitment.

Effect of River Valley Projects

The annual runoff in the Ganga basin, after allowance for evapotranspiration, soil seepage and groundwater recharge, is about 469 billion m^3. Of this 85 billion m^3 of water is diverted by canal projects and by hydro-electric and storage reservoirs for irrigation, power and flood control. Canal projects account for a little over 60 % of the impounded water. The diversion of water has caused large-scale changes in the channel bed, and hydrography of the river in terms of flow, flow-rate, flood-rhythm and regime. Hydraulic structures have changed river morphometry, increased bank erosion and created barriers for migratory fishes. The construction of flood-control dykes and levees in flood-prone low-lying areas has deprived the major carps of their extensive breeding habitats, previously available in a network of interlaced channels connected with the Kosi River (David 1959) and the floodplains of the Kosi, Gandak, Rapti, Sarju, and other tributaries. In 1965–66, the oxbow lakes of the Burhi Gandak sub-basin in Champaran district alone covered an area of 36 000 ha and provided a fishery of 2 900 $t \cdot yr^{-1}$; however, this level of production was already much lower than that of earlier years (Shetty and Malhotra 1983). The major carp fishery has declined in many oxbow lakes, as they change to marsh. The ecology of these oxbow lakes is further affected by sluice gates on inlet and outlet channels, which are operated more to serve agriculture than fisheries. Canal projects and flood control measures are two major factors that are especially responsible for the destruction of breeding habitat for major carps. These factors are largely responsible for diminished productivity of oxbow lakes which are a major source of the fisheries of Bihar, West Bengal and Eastern Uttar Pradesh.

Impact of Agriculture on the River System

About 62 % of the Ganga basin is under cultivation. At present, agriculture uses annually about 1.15×10^6 t of chemical fertilizers, mostly N-based, and 2 600 t of pesticides, a good portion of which are non-degradable chlorinated organics. About 27 billion m^3 of waste water carrying toxic pesticide residues, and chemical nutrients from fertilizers drain from irrigated fields into the river system (Das Gupta 1984). The highly erodible alluvial soils of agricultural areas also add to the suspended sediment loads of the river.

Land-Use Patterns

Land-use patterns in a watershed influence runoff, river hydrography and sediment load. Forest covers only 14.3 % of the Ganga basin; the national average is 20.14 %. The reduction of forest cover has been due largely to massive felling of trees in recent years. In Bihar, which contributes the major part of the discharge of the Ganga River, forest cover is only 2.4 %. Deforestation is the reason for the excessive silt load in most of the Himalayan tributaries, a load which has increased rates of siltation downstream in oxbow lakes, floodplains, sloughs and backwaters. Based on information on the Potomac River basin, Patrick (1972) observed that when forest cover was reduced from 80 % to 20 %, the sediment yield increased eight times. Reduction in forest cover has led to a great increase in both the dissolved and particulate solids in the Ganga River system (Rao 1979). The turbidity level is very high (Table 4) and the sediment load has reduced the effective photosynthetic zone and diminished benthic productivity.

Effects of Pollution

A survey by the Central Pollution Control Board in 1981 showed that as many as 317 industrial plants are located on the banks of the Ganga and its tributaries, and that only 30 % have any control measures. The 29 cities and towns on the banks contribute nearly 90 % of the sewage load to the river. There are a number of thermal power plants, including giant plants at Kanpur, Barauni and Bandel. Whereas suspended BOD is neutralized within a 100-km of its source to the main river, settleable BOD, derived from organic waste water from agro- and forestry-based industries and from fly ash from thermal power plants, has had deleterious effects on aquatic benthic invertebrates. Invertebrate numbers decrease progressively from 3 500 m^{-2} at Kanpur in the upper Ganga to 10 m^{-2} at Diamond Harbour on the lower Ganga. Coal-wash plants in the Durgapur–Assansol area of the Damodar have a similar effect. Organic enrichment also has a detrimental effect on insect abundance. In addition, toxicity of metallic ions appears to have further diminished benthic abundance in the lower Ganga, following changes in the salinity regime when two-thirds of the deltaic stretch became freshwater. The comparatively low level of the catfish population of the Ganga system may be attributed in part to this phenomenon.

About 1.5 billion m^3 of waste washings from industries, domestic and municipal sewage are discharged into the Ganga River system annually (Das Gupta 1984). The BOD load at major points of discharge, such as Durgapur, Kanpur, Calcutta and Delhi, is typically in the range 40–130 $t \cdot d^{-1}$. The impact of forest industry wastes on aquatic life including fish is most severe in streams and tributaries with low rates of summer flow (less than 400 $m^3 \cdot s^{-1}$), especially in the Gomti, Kali, Daha, Suvaon rivers. Many oxbow lakes which serve as breeding habitats and brood stock refugia are also influenced by cultural eutrophication caused by high nutrient loads from agricultural sources and phosphate-enriched detergents in domestic sewage. This eutrophication has lead to the choking of these aquatic habitats by water hyacinth and other undesirable plants. Many oxbow lakes now support only airbreathing fish and some have become totally unsuitable for fish life.

Multiple Use of Water Resources

While agriculture, power production, industrial development, flood control, domestic water supply, and navigation receive priority consideration, the basic water requirements necessary to protect breeding habitat and to provide summer shelter for fish brood stocks have received low priority. There is lack of planning for the optimal allocation of Ganga River water.

Impact of Environment of Fish Stocks

Changes in hydrography arising from canal projects and flood control measures and changes in river morphometry have reduced considerably the extent of breeding habitat and have depressed recruitment of major carps even though these species show high fecundity: 20 000–228 000 eggs for *Catla catla*; 109 000–413 000 eggs for *Labeo rohita*; 288 000–438 000 eggs for *Labeo calbasu*, and 140 000–152 000 eggs for *Cirrhina mrigala* (Sukumaran 1969). Poor recruitment has led to a reduced fishery for these species (Table 9) except for *L. calbasu*.

Labeo calbasu ranks lowest in terms of quality, value and economic importance among major carps, but has shown an increase in yield between 116 and 640% at all sampling centres. The miscellaneous group also showed increased yields from the Bhagalpur and Allahabad stretches of the Ganga and Yamuna rivers.

Major carp species (*C. mrigala*, *L. rohita*, and *C. catla*) share a similar trophic level with the miscellaneous group (excluding its catfish components); these species also share breeding habitats with *L. calbasu*. With increasing populations already established in the river system, *L. calbasu* could further increase in future years at the cost of *C. mrigala*, *L. rohita* and *C. catla* because *L. calbasu* controls the shrinking breeding habitat.

The dominance of a single species of major carp arising from limited breeding habitat has already been observed in reservoirs, e.g. *L. calbasu* in Bhavanisagar and *C. catla* in Rihand (Natarajan 1979). The restricted breeding habitat may also lead to hybridization among major carps (Hubbs 1955; Natarajan et al. 1976). The collapse of homeostatic mechanisms that regulate population numbers within a trophic level following the depression of recruitment of three species of major carps, and the availability of a larger food supply, make it possible for the miscellaneous group of uneconomic species to increase further their population density. This, in turn, would normally favour increasing dominance of catfishes located at a higher trophic level, especially *M. aor* and *M. seenghala* which breed mostly in summer and are thus independent of the requirement of inundated breeding habitats. The increase of catfishes, however, is likely to be limited by continuing deterioration of river-bed conditions caused by accumulation of sewage sludge and industrial organic wastes. These trends imply further changes in fishery structure and foreshadow a diminished fish yield from the Ganga River system.

Effects of Hydraulic Structures on Migratory Fishes

The longrange migrant *Hilsa ilisha* forms the basis of an important fishery in the Ganga River system with an annual production of about 1 500 t from the delta and up to 100 t from the middle reaches. The fish is vulnerable to any hydraulic structure that impedes its migrations, particularly in the deltaic stretches of the river. The natural migratory range of the fish is 1 500 km from the Hooghly estuary to Allahabad on the Ganga. The 1975 construction of a barrage at Farakka at the head of the Bhagirathi and Padma tributaries of the Ganga, some 470 km from the river mouth, has not affected the hilsa fishery in the tidal stretch of the delta. However, the barrage has nearly eliminated the riverine fishery upstream of Farakka on the main stem of the Ganga, a fishery which was based on runs of both Padma and Hooghly stocks. After construction of the barrage at Farakka, the Bhagirathi River, a non-tidal stretch of the delta, was connected with the main river upstream by a feeder canal loop with a head regulator at the upstream end. There is a second barrage (Jangipur barrage) on the Bhagirathi upstream where the main river divides into the Hooghly and Padma rivers; this dam ensures water flow to the Hooghly via the feeder canal loop while the Padma has direct access to Farakka barrage (Fig. 1). The Farakka barrage has a fish lock, which is ineffective as a pass from the Padma. The proposed navigation lock connecting the feeder canal with main river upstream is likely to facilitate hilsa migration from Hooghly to the main river and restore some part of the lost upstream hilsa fishery. It is unlikely that the riverine hilsa fishery will regain its earlier importance because the Padma run will remain unavailable.

Pantulu et al. (1966) reported that hilsa ceased to migrate up the Damodar River, a tributary of the Hooghly, after construction of dams (DVC dams), a barrage (Durgapur), and a weir (Anderson weir). The migratory range of fish is also restricted to 40 km in the Rupnarain River contributing to the decline of the hilsa fishery in the Hooghly.

Hydraulic structures in upper reaches of the river obstruct migration of mahseers (*Tor* spp.) that move from lowland to upland reaches for breeding. Shetty and Malhotra (1983) reported the decline of *Tor tor* along with other fishes following construction of a barrage at Tribeni on the Gandak River. The impact of canal projects on the other northern tributaries of the Ganga needs to be investigated. Hydroelectric dams on the upper reaches of these rivers may also prove detrimental to mahseer, catfish (*B. bagarius*) and the carps (*Labeo dero* and *L. dyocheilus*). Fish lifts may not be economical in the case of high dams, but populations could still be sustained through artificial propagation.

Barrages at Son, Okhla, and Farakka are also known to impede major carp migrations for breeding. For example, the yield of major carp has been reduced in the lower Ganga following construction of Farakka to about 50 % of the 1964 level (Jhingran and Ghosh 1978).

The Impact of Aquaculture on Riverine Fishery

The Ganga River system has been looked upon as an unlimited source of supply of major carp "seed" for use in Indian aquaculture. The country's aquaculture strategy has been based on this premise since the mid-1960's, with spawn-collecting devices, surveys, and exploitation in different river systems taking a major share of research and development resources (Jhingran 1968). The Ganga River and its tributaries were surveyed for carp spawn solely to supply the aquaculture sector. According to the Fish Seed Committee Report (Gov. of India; Dep. of Agric. 1966), the Ganga River system provided about 90 % of carp seed for aquaculture in 1964. The annual riverine carp spawn target was 3 744 million individuals by 1979. The draft 10-yr aquaculture plan set a target for riverine carp spawn in the order of 6 000 million• yr^{-1} by 1984 (George and Sinha 1975). Such targets are set from time to time, even as major carp populations continue to diminish in size and yield, and spawn quality continues to deteriorate, with minor carps and other species dominating the composition of spawning stocks. Details of a carp seed survey in different river systems are in Table 12, and the percentage of major carp spawn in Table 13.

At present, minor carps and miscellaneous groups contribute about 58 % of the spawn. The spawn quantity index of the main Ganga is about a quarter that of the Yamuna. The Bihar stretch of the Ganga, which now leads the country in carp seed production, is, ironically, witnessing a decline in the major carp fishery with miscellaneous species forming about 60 % of the yield. The country will face the prospect of losing prime genetic material from the major carps of the Ganga River system unless a total ban on collection of eggs, spawn, fry and fingerlings of major carps from the river is enforced without delay. Dependence on riverine spawn for aquaculture has little or no justification when the country has sound technology for cultivating major carp brook stocks and many hatcheries are being established with government assistance.

Adaptations and Their Significance in Modified Ecosystems

Much of the work on fish systematics in the country is based on morphological and meristic characters. Little work has been done on cytogenetics, karyomorphology and serological and biochemical parameters of fish genetic resources. Still less, indeed, is our knowledge of populations with adaptations suited to specialized habitats. Manmade impoundments and natural floodplain waterbodies

TABLE 12. Indices of carp spawn (hatchling) abundance and quality of the Ganga River system during the years 1964–70. Source of data: Jhingran, V.G. 1975. Fish and Fisheries of India, Hindustan Publishing Corporation, Delhi.

			Index of spawn quality (%)			
Year of observation	Centre (State)	Main river/ tributary of Ganga River	Index of spawn quantity (mL)	Major carps	Minor carps	Others
1964	Kishanpur (U.P.)	Yamuna	7355.60	85.30	14.60	0.10
1964	Mahewa–Jamunapur (U.P.)	Yamuna	4402.00	72.30	27.40	0.30
1964	Tajpur (U.P.)	Ramganga	3351.20	2.80	96.70	0.50
1964	Sardanagar (U.P.)	Ramganga	965.60	5.90	94.00	0.10
1964	Balaha (U.P.)	Tons	28.40	—	—	—
1965	Anwara (U.P.)	Yamuna	3493.00	81.00	19.00	—
1965	Dhumanpura (U.P.)	Yamuna	2200.00	35.00	24.00	41.00
1965	Bansi (U.P.)	Rapti	4715.00	77.70	21.60	0.70
1965	Dhundhua (Bihar)	Son	637.00	3.50	94.90	1.60
1965	Dangwar (Bihar)	Son	2417.00	25.20	74.80	—
1966	Majhawali (Haryana)	Yamuna	784.00	18.60	80.84	0.56
1966	Mant (U.P.)	Yamuna	17.30	26.30	72.60	1.10
1966	Ghagraghat (U.P.)	Ghagra	228.40	7.40	92.60	—
1966	Khagaria (Bihar)	Burhi Gandak	—	—	65.28	34.72
1966	Babuaghat (Bihar)	Kosi Khanua Dhar	664.00	35.10	46.50	18.30
1966	Mehdi Jha jha (Bihar)	Badua	—	26.10	73.90	—
1967	Nethla (U.P.)	Yamuna	6006.10	7.00	86.40	6.60
1967	Salempur (U.P.)	Gomati	1373.60	26.40	73.60	—
1967	Tonk (Sopari) (Rajasthan)	Banas	1801.00	81.50	17.70	0.80
1968	Negria (Rajasthan)	Banas	1531.50	59.40	40.40	0.20
1968	Nanamau (U.P.)	Ganga	807.60	76.30	23.10	0.60
1968	Deolan (U.P.)	Yamuna	239.00	83.70	15.20	1.10
1968	Mahewapatti (U.P.)	Yamuna	601.00	18.20	78.80	3.80
1969	Mahewapatti (U.P.)	Yamuna	1098.00	52.20	47.40	0.40
1969	Bahiara (Bihar)	Son	252.00	88.50	11.50	—
1970	Ahirauli (Bihar)	Ganga	552.00	85.49	—	—

TABLE 13. Frequency distribution of index of spawn quality (%) based on a sample of 26 centres on Ganga River system during 1964-70.

Index range of spawn quality (%)	Major carp No. of centres	Percentage
0-24.99	9	34.61
25.00-49.99	6	23.08
50.00-74.99	3	11.54
75.00-99.99	8	30.77
	Total: 26	

perform as biological filters helping to segregate and differentiate ecological populations. An example of this is provided by the riverine major carp *Catla catla* which has long been considered a monotypic species in the literature. Natarajan et al. (1977), on the basis of studies carried out during 1974-77 in the Rihand reservoir on the Son River, reported the occurrence of three ecological populations of this species distinguished from each other as much by their diverse ecological niches as their morphology.

Pangasius pangasius also displays racial differentiation; one race breeds in the estuary (Pantulu 1962), a second in the river (David 1963), a third in lakes and reservoirs (Natarajan 1979), and a fourth race which has developed an ability to breath air is found in deoxygenated floodplain waters (Thakur, CIFRI Centre, Dhauli, Bhubaneswar, pers. com.). *Hilsa ilisha* has diverse ecological population units. Pillay et al. (1962) reported the existence of four distinct races or ecological populations of *H. ilisha*, two of which are estuarine (Padma and Hooghly estuaries) and two which are fluviatile in the Ganga River system. The Hilsa of the Narbada River shows adaptations to lacustrine habitat and is now established in the Ukai reservoir (Workshop Report, All India Coordinated Res. Proj. on Ecol. and Fish. of Freshw. Reservoirs, CIFRI/ICAR 1983). The mahseer, *Tor putitora*, a riverine species with long upstream migrations, also shows adaptations to lacustrine habitat, becoming established in the Kumaon lakes where migrations are limited to only a few kilometres.

Studies on ecological populations and stocks showing ecophysiological adaptations of riverine species need to be intensified with a view to restructuring the species mix and enhancing fisheries in modified ecosystems.

Fishery Management

India has a federal system of Government, so fisheries is a state responsibility. Each of the seven states in the Ganga River basin follows its own priorities. A common property approach prevails for much of the system. Elsewhere, management is limited to the auction of fishing rights for river stretches, without restriction on size of catch, size of fish or fishing season. Large-scale capture of brood stocks while migrating during monsoon, large-scale poaching, destruction of fish in their summer refugia, and large-scale destruction of fry and fingerlings for consumption are more a rule than an exception (Jhingran and Chakraborty 1958; David 1959; Shetty and Malhotra 1983).

In the changing river with its depletion of stocks, there is a need for reappraisal of prevailing practices of exploitation. More purposeful management aimed at rehabilitation of the depleted fishery for major carps and an enhancement of the fishery in line with the potential production of the river system are needed.

Recruitment must be the main focus of any new management approach, including better management of breeding habitat and protection for fry, fingerlings and brood-stock. Fishing effort, mesh sizes, and minimum lengths at entry into the fishery also have to be regulated. The following are proposed as measures in support of this goal:

(i) Selected oxbow lakes, floodplains, low-lying areas and backwaters known to be breeding grounds of major carps should be listed and declared as breeding sanctuaries. Hydraulic structures, embankments or levees should be prohibited to allow free entry of fish into these breeding habitats. Some oxbow lakes known for major carp fisheries may be designated and managed as brood stock refugia;

(ii) The natural river bed has many deep areas which provide shelter for fish in summer during low water levels. Irrigation projects have caused several of these areas to become more or less dry in summer, exposing them to large-scale slaughter of fish by poachers. Irrigation projects must be managed to ensure that these pools retain adequate water;

(iii) Oxbow lakes of the Burhi Gandak in the Champaran district provide an annual fishery of some 3 000 t in contrast to the 1 200 t from the main Ganga from Bulandshaher to Farakka (1 500 km). Several of these oxbow lakes are already suffering from artificial eutrophication. Sewage discharges, human settlement and utilization of foreshore areas for agriculture are among the encroachments that should be controlled to safeguard the oxbow lake fisheries. The strengthening of embankments and raising of dykes on the Kosi, Gandak, and other tributaries have isolated flood areas, disconnected interlaced channels and disrupted the natural carp breeding habitats. Low dykes are recommended to ensure the minimum flood areas needed for breeding of major carps;

(iv) Because of fishing, there is large-scale destruction of brood stocks of the Hooghly hilsa in the feeder canal and near the head regulator of the feeder canal at Farakka. Major carp are likewise heavily fished near other barrages. Fishing within a 50-km reach downstream of hydraulic structures needs to be strictly limited;

(v) Considering the alarming decline in yield of major carps and the continuing deterioration of the quality of fish spawn, a ban should be imposed on major carp spawn collection from the Ganga River system. In addition, a ban should be imposed on the collection of major carp fry and fingerlings for consumption or sale;

(vi) Closed seasons should be enforced between June and July in West Bengal, July and August in Bihar, and August and September in Uttar Pradesh. A minimum mesh size of 75 mm should be enforced to protect fishes less than 2 years old, the age at which major carps attain maturity;

(vii) Intensive stocking of *L. rohita*, *C. mrigala*, and *C. catla* would be required if the rehabilitation management measures proposed above fail to achieve the desired objectives. Stocking of hilsa and mahseer (*T. tor*) has to be undertaken on a large scale to revive the fisheries in affected stretches;

(viii) Use of set barrier nets should be banned to protect migratory brood stock;

(ix) Fishing effort on the main Ganga River may need to be reduced after a detailed inventory of present fishing effort and practice. The yield in the Ganga remains the same as that of the Yamuna although the effective fishing gear density of the Ganga (in terms of drag nets• km^{-1}) is three times as high as in the Yamuna. A licensing system must be adopted, renewable every year, to exercise control over fishing gear and craft as indicated in the Report by the National Commission on Agriculture (Department of Agriculture 1976);

(x) Only 30 % of industries on the Ganga River system adopt any control measures. Fly ash, coal particles, agro-industrial organic wastes and settleable sewage have diminished benthic productivity. While sewage is taken care of through the Ganga Action Plan Programmes, other industrial wastes need control measures;

(xi) Management of the fisheries of the Ganga River implies the setting up of institutional arrangements for development, implementation, policy and planning of management of fish stocks, production, marketing and distribution. There exists a Central Board of Fisheries and a Central Board for Prevention and Control of Water Pollution, at the policy and planning level. However, there has to be an interstate compact, agency or river commission whereby the seven states of the basin can frame policies on water and biological resources of the river. Isolated institutional frameworks at the levels of implementation and development alone are totally inadequate.

(xii) There is need for cooperation between India and Nepal in the management of migratory stocks of mahseer and between India and Bangladesh in the management of *H. ilisha*. In addition, there is a need for understanding between Nepal and India on the introduction of exotic fishes as these, especially grass carp, silver carp and big head which have the potential to alter drastically the existing biological structure of the river fishery and to accelerate the process of elimination of many species like *Catla catla*, *L. rohita* etc.

(xiii) Few dependable data exist on catch and fishing effort based on reliable sampling methodologies relating to the Ganga tributaries, other than for the Yamuna and oxbow lakes. This deficiency has to be rectified, preferably by establishing a 5-yr census of fishing effort of the Ganga and its major tributaries to assess impact on stock abundance and to facilitate proper planning and management of fish stocks.

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References

CIFRI/ICAR. 1980. Annual report, Barrackpore, West Bengal, India. 108 p.

1981. Annual report, Barrackpore, West Bengal, India. 132 p.

1982. Annual report, Barrackpore, West Bengal, India. 105 p.

1983. Seventh Workshop. All India coordinated research project on ecology and fisheries of freshwater reservoirs, Barrackpore, West Bengal, India.

1985. Annual report, Barrackpore. West Bengal, India. 133 p.

DALELA, R.C. 1984. Deteriorating nation's rivers, p. 1–12. *In* R.C. Dalela and U.H. Mane [ed.] Proceedings of the National Symposium on Assessment of Environmental Pollution. Acad. Environ. Biol. India.

DAS GUPTA, S.P. 1984. Basin sub-basin inventory of water pollution: the Ganga Basin Part II. Central Board for the Prevention and Control of Water Pollution, New Delhi. ADSORBS/7/1982-83. 204 p.

DAVID, A. 1959. Observations on some spawning grounds of the Gangetic major carps with a note on carp seed resources in India. Indian J. Fish. 6(2): 327–341.

1963. Studies on fish and fisheries of the Godavari and Krishna river systems. Proc. Nat. Acad. Sci. India 33B(2): 263–386.

DAY, F. 1889. The fauna of British India, including Ceylon and Burma. Fishes 1. Taylor and Francis, London. 187 p.

DEPARTMENT OF AGRICULTURE, GOVERNMENT OF INDIA. 1966. Report of the Fish Seed Committee, New Delhi. 211 p.

1976. Report of the National Commission on Agriculture, Pt. VIII. Fisheries, New Delhi. 270 p.

GEORGE, P.C., AND V.R.P. SINHA. 1975. Ten-year aquaculture development plan for India 1975–84. 2nd Reg. Workshop Aquaculture Plann., Bangkok, Thailand. FOA/UNDP. p. 1–33.

GHOSH, B.B., M.K. MUKHOPADHYA, AND. M.M. BAGCHI. 1982. Some observations on bio-accumulation, toxicity, histopathology and haemotology of some fishes in relation to heavy metal pollution in the Hooghly estuary between Nabadwip and Kakdwip. First National Environment Congress. Indian Environmental Congress Assoc. and Dep. of Environ., Gov. of India. p. 25.

GUPTA, S.D, AND. A.G. JHINGRAN. 1974. Ageing *Labeo calbasu* (Hamilton) through its scales. J. Inl. Fish. Soc. India 5: 126–128.

HORNEL, J. 1924. The fishing methods of Ganges. Mem. Asiat. Soc. Bengal 8(3): 199–237.

HUBBS, G.L. 1955. Hybridization between fish species in nature. Syst. Zool. 1(1): 20.

JHINGRAN, A.G., AND. K.K. GHOSH. 1978. The fisheries of the Ganga River system in the context of Indian aquaculture. Aquaculture 14: 141–162.

JHINGRAN, V.G. 1956. The capture fishery of River Ganga at Buxar (Bihar, India) in the years 1952–54. Indian J. Fish. 3: 197–215.

1959. Studies on the age and growth of *Cirrhina mrigala* (Ham.) from the River Ganga. Proc. Nat. Inst. Sci. India. 25B(3): 107–137.

1968. Riverine fish seed resources and their exploitation in India. ICAR/CIFRI Seminar on production of quality fish seed for fish culture. Central Inland Fisheries Research Institute, Barrackpore, India. p. 56–80.

1975. Fish and fisheries of India. Hindustan Publishing Corporation, Delhi. 954 p.

JHINGRAN, V.G., AND. R.D. CHAKRABORTY. 1958. Destruction of major carp fingerlings in a section of River Ganga and its probable adverse effects on fish production. Indian J. Fish. 5(2): 291–299.

KAMAL, M.Y. 1969. Studies on the age and growth of *Cirrhina mrigala* (Ham.) from the River Yamuna at Allahabad. Proc. Nat. Inst. Sci. India 35B(1): 72–79.

KARAMCHANDANI, S.J., AND. M.P. MOTWANI. 1955. Early life history, bionomics and breeding of *Rita rita* (Hamilton). J. Zool. Soc. India 7(2): 115–126.

1956. On the larval development of four species of freshwater catfishes from the River Ganga. J. Zool. Soc. India 8 (1): 19–34.

KHAN, H.A., AND. V.G. JHINGRAN. 1975. Synopsis of biological data on Rohu *Labeo rohita* (Hamilton, 1822). FAO Fish Synops. (III), 100 p.

KIMBAL, H.H. 1935. Intensity of solar radiation at the surface of the earth and its variations with latitude, altitude, seasons and time of the day. Mon. Weather Rev. 63(1): 1-4.

KURIAN, C.V., AND. V.O. SEBASTIAN. 1982. Prawn and prawn fisheries of India. Hindustan Publishing Corporation, Delhi, 286 p.

MENON, A.G.K. 1974. A check list of Himalayan and the Indo-Gangetic plains. J. Inl. Fish. Soc. India, (Spec. Publ. No. 1): 1-136.

NATARAJAN, A.V. 1976. Ecology and the state of fishery development in some of the man-made reservoirs in India. Symposium on the development and utilization of inland fishery resources. Proc. Indo-Pacific Fish. Coun. Section III 17th Session, Colombo, p. 258-267.

1979. Planning strategies for development of reservoir fisheries in India. Madras J. Fish. 8: 69-77.

NATARAJAN, A.V., V.R. DESAI, AND. D.N. MISHRA. 1976. On the natural occurrence of the inter-generic Catla × Rohu hybrid in Rihand (U.P.) with an account of its potential role in reservoir fisheries development in India. J. Inl. Fish. Soc. India 8: 83-90.

NATARAJAN, A.V., V.R. DESAI, D.N. MISHRA, AND. N.P. SRIVASTAVA. 1977. Some new light on population ecology of the Gagnetic major carp. *Catla catla* (Ham.) from Rihand reservoir (U.P., India). Matsya 3: 46-59.

NATARAJAN, A.V., AND. A.G. JHINGRAN. 1963. On the biology of *Catla catla* (Ham.) from the river Yamuna. Proc. Nat. Inst. Sci. India, 29B(3): 226-255.

NATARAJAN, A.V., M. RAMAKRISHNAIAH, AND. M.A. KHAN. 1975. The food of trash fishes in relation to major carps in Konar and Tilaiya reservoirs (Bihar). J. Inl. Fish. Soc. India. 7: 65-75.

ODUM, H.T. 1957. Trophic structure and productivity of Silver Spring, Florida. Ecol. Monogr. 27: 55-112.

PAHWA, D.V., AND. S.N. MEHROTRA. 1966. Observations on fluctuations in abundance of plankton in relation to certain hydrological conditions of River Ganga. Proc. Nat. Acad. Sci. 36: 157-189.

PANTULU, V.R. 1962. On the use of pectoral spine for the determination of age and growth of *Pangasius pangasius* (Hamilton Buch.). J. Cons. 27(2): 192-216.

PANTULU, V.R., K. ALAGARAJA, AND B.S. BHIMACHAR. 1966. Fisheries of the Damodar Valley in relation to construction of dams. Proc. Nat. Inst. Sci. India 32B(5&6): 191-207.

PATHAK, V., S.B. SAHA, AND. M.J. BHAGAT. 1985. Patterns of energy utilization and productivity in beel ecosystems. J. Hydrobiol. 1(2): 47-52.

PATRICK, R. 1972. A commentary on "What is a river", 67-74. *In* R.T. Oglesby, C.A. Carlson and J.A. McCann [ed.]. River Ecology and Man. Academic Press, New York, NY.

PILLAY, T.V.R., S.R. PILLAY, AND K.K. GHOSH. 1962. A comparative study of the populations of the Hilsa, *Hilsa ilisha* (Ham.) in Indian water, p. 62-104. *In* Proc. Indo-Pacific Fish. Coun. Sec. II.

QASIM, S.Z., AND. A. QAYYUM. 1962. Spawning frequencies and breeding seasons of some freshwater fishes with special reference to those occurring in the plains of Northern India. Indian J. Fish. 8(1): 24-43.

RAJYALAKSHMI, T. 1980. Comparative study of the biology of the freshwater prawn *Macrobrachium malcolmsonii* of Godavari and Hooghly river systems. Proc. Indian Nat. Sci. Acad., B. 45(1): 77-89.

RAO, K.L. 1979. India's Water Wealth: Its assessment, uses and projection. 2nd ed. Orient Longman Limited, New Delhi. 267 p.

RAY, P., AND. A. DAVID. 1966. Effects of industrial wastes and sewage upon chemical and biological composition and fisheries of the River Ganga at Kanpur (U.P.) Environ. Health 8: 307-339.

RAY, P., S.B. SAHA, AND. R.K. BANERJI. 1981. A case study of use of Calcutta municipal wastes for fish culture in Bidyadhari-Kulti complex, West Bengal, p. 99-108. *In* International Symposium on Water Resources, Conservation, Pollution and Abatement. Dep. of Civil Eng. Univ. Roorkee Programme.

RAY, P., S.B. SINGH, AND. K.L. SEHGAL. 1966. A study of some aspects of ecology of the River Ganga and Yamuna at Allahabad. Proc. Nat. Acad. Sci. 36: 235-272.

SHETTY, H.P.C., AND. J.C. MALHOTRA. 1983. A report on the survey of North Bihar in relation to effects of Gandak and Kosi River valley projects on the fisheries of the area. Survey Report 7. Cent. Inl. Fish. Res. Inst., Barrackpore. 30 p. (mimeo).

SHETTY, H.P.C., S.B. SAHA, AND. B.B. GHOSH. 1916. Observations on the distribution and fluctuations of plankton in the Hooghly-Matlah estuarine system with notes on their relation to commercial fish landings. Indian J. Fish. 8: 326-363.

SUKUMARAN, K.K. 1969. Growth, maturation and fecundity of cultivated fishes. FAO/UNDP Regional Seminar on Induced Breeding of Cultivated Fishes, Calcutta. Rome, FAO: FRI/IBCF/5. 5: 52.

WISHARD, S.K. 1974. "Rok" fishing and its possible effects on the capture fishery of River Yamuna in Agra district (U.P.). Indian J. Fish.

Fisheries Resources of the Pearl River and Their Exploitation

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Abstract

Liao, G. Z., K. X. Lu, and X. Z. Xiao. 1989. Fisheries resources of the Pearl River and their exploitation, p. 561–568. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

A survey of the Pearl River between 1982 and 1984 indicates 381 species of fish were present, of which 262 inhabit freshwater and 119 inhabit brackish water or are diadromous. The fish community appears highly diverse. The freshwater fish are dominated by cyprinids which account for 62.6% of the total number of species. Fifty-three species are of commercial importance, including seven major cultivated species — grass carp, bighead carp, silver carp, black carp, mud carp, common carp and crucian carp. Estuarine fishes are dominated by Perciformes (63 species) and Clupeiformes (17 species) and include 16 orders and 14 families.

The greatest number of fish species (209) are found in the middle section (Guangxi), with 161 in the downstream Guangdong section, 115 in the upstream Yunnan section, and 95 in the Guizhou section. Fish production is higher in the Guangdong section (8 308.5 t•yr^{-1} in 1982) than in the Guangxi section (3 147.9 t•yr^{-1}). Analysis of production in different years shows that mean annual catches reached a peak in the 1950's at 10 367 t•yr^{-1}). Since the 1960's annual catches have been declining; early 1980's catches were only 6 463.7 t•yr^{-1}, representing a decrease of 37.7%.

Human interventions have caused great changes in the Pearl River over the past 20 yr. Water pollution and damming have contributed to the decline in commercial fish populations. Overfishing coupled with the use of harmful gears, such as electric shocking, bombing and poisoning has led to the reduction in abundance of certain fish species.

A great effort is needed to restrict overexploitation of the fish stocks of the Pearl River. Controls are also needed to stop pollution of the waters of this river and its tributaries. Improved management would prevent further deterioration of the aquatic environment, stabilize the fish population and increase fish production.

Résumé

Liao, G. Z., K. X. Lu, and X. Z. Xiao. 1989. Fisheries resources of the Pearl River and their exploitation, p. 561–568. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Un inventaire de la rivière Pearl réalisé entre 1982 et 1984 indique qu'il s'y trouvait 381 espèces de poisson, dont 262 fréquentent les eaux douces et 119, les eaux saumâtres ou qui sont diadromes. La communauté de poissons semble très diversifiée. Chez les poissons d'eaux douces, il y a dominance des cyprinidés, qui représentent 62,6% du nombre total d'espèces. Cinquante-trois espèces sont importantes sur le plan commercial, parmi lesquelles on compte sept principales espèces d'élevage, soit la carpe de roseau, la carpe marbrée, la carpe argentée, la carpe noire, la carpe de vase, la carpe commune et le carassin. Les poissons d'estuaire sont dominés par les perciformes (63 espèces) et par les clupéiformes (17 espèces) et comprennent 16 ordres et 14 familles.

Le plus grand nombre d'espèces de poissons (209) se trouvent dans le tronçon intermédiaire (Guangxi), 161 dans le tronçon d'aval de Guangdong, 115 dans le tronçon d'amont de Yunnan et 95 dans le tronçon de Guizhou. La production de poisson est plus élevée dans le tronçon de Guangdong (8 308,5 t•an^{-1} en 1982) que dans celui de Guangxi (3 147.9 t•an^{-1}). L'analyse de la production au cours de différentes années montre que les prises annuelles moyennes ont atteint un sommet dans les années 50 avec 10 367 t•an^{-1}. Depuis les années 60, les prises annuelles ont diminué; au début des années 80, les prises n'ont été que de 6 436,7 t•an^{-1}, ce qui représente une baisse de 37,7%.

Les interventions humaines ont provoqué de grands changements dans la rivière Pearl au cours des 20 dernières années. La pollution de l'eau et l'endiguement ont contribué à faire baisser les populations de poissons commerciaux. La surpêche, jointe à l'utilisation d'engins nuisibles, comme les chocs électriques, les explosifs et le poison, ont mené à la diminution de l'abondance de certaines espèces de poisson.

Il faut déployer de grands efforts pour limiter la surexploitation du stock de poisson de la rivière Pearl. Des mesures de contrôle sont également nécessaires pour mettre un frein à la pollution des eaux de cette rivière et de ses tributaires. Une meilleure gestion empêcherait une détérioration plus grande du milieu aquatique, stabiliserait la population de poisson et en augmenterait la production.

Introduction

The Pearl River, 21°31'N and 115°55'E, is the largest river in Southern China with a drainage area of some 453 690 km^2 and a main channel length of 2 129 km. The river system is comprised of three main rivers, the West River, North River, and East River, which discharge through a common delta into the South China Sea. The river flows from west to east through four provinces, Yunnan, Guizhou, Guangxi, and Guangdong (Fig. 1). It has a total annual discharge of 341.2 billion m^3 and an average annual flow of 11 000 m^3•s^{-1}, making it China's second largest river after the Yangtze River.

The Pearl River is a subtropical stream. Mean annual temperature is greater than 20°C. Maximum air temperatures in summer can reach 42°C, yet temperatures fall as low as −6.9°C in winter. Rainfall in the region is heavy, between 1 000 and 2 000 mm per year. Because of the abundance of fish food organisms and fish stocks, the Pearl River has favourable conditions for fisheries. However, the status of the fishery resources of the Pearl River has not been studied, the environmental protection for fisheries purposes has been ignored, and rational exploitation of fish resources neglected. This inaction has resulted in a noticeable reduction in abundance of certain commercially valuable fish, and now some species are in danger of disappearing.

A comprehensive survey was carried out between 1981 and 1983 by nine research institutes and universities in four provinces[1] to determine the major factors influencing changes in fish stocks and to provide the basis for enhancement and rehabilitation strategies for the fishery resource in the Pearl River. This paper summarizes the results of this investigation[2].

Physical and Chemical Characteristics

Major physical and chemical characteristics of the Pearl River are summarized in Table 1.

Water temperature varied annually between 6.5°C and 34°C. The mean annual water temperature was more than 20°C. Secchi depth varied with season and section, ranging between 0.1 and 4.5 m in the dry season and between 0.02 and 0.9 m in the flood. Dissolved oxygen concentrations were rather high, mostly ranging between 5 and 7 mg•L^{-1}, and were closely related to the degree of contamination of the water. The greater the water pollution, the less the dissolved oxygen concentration.

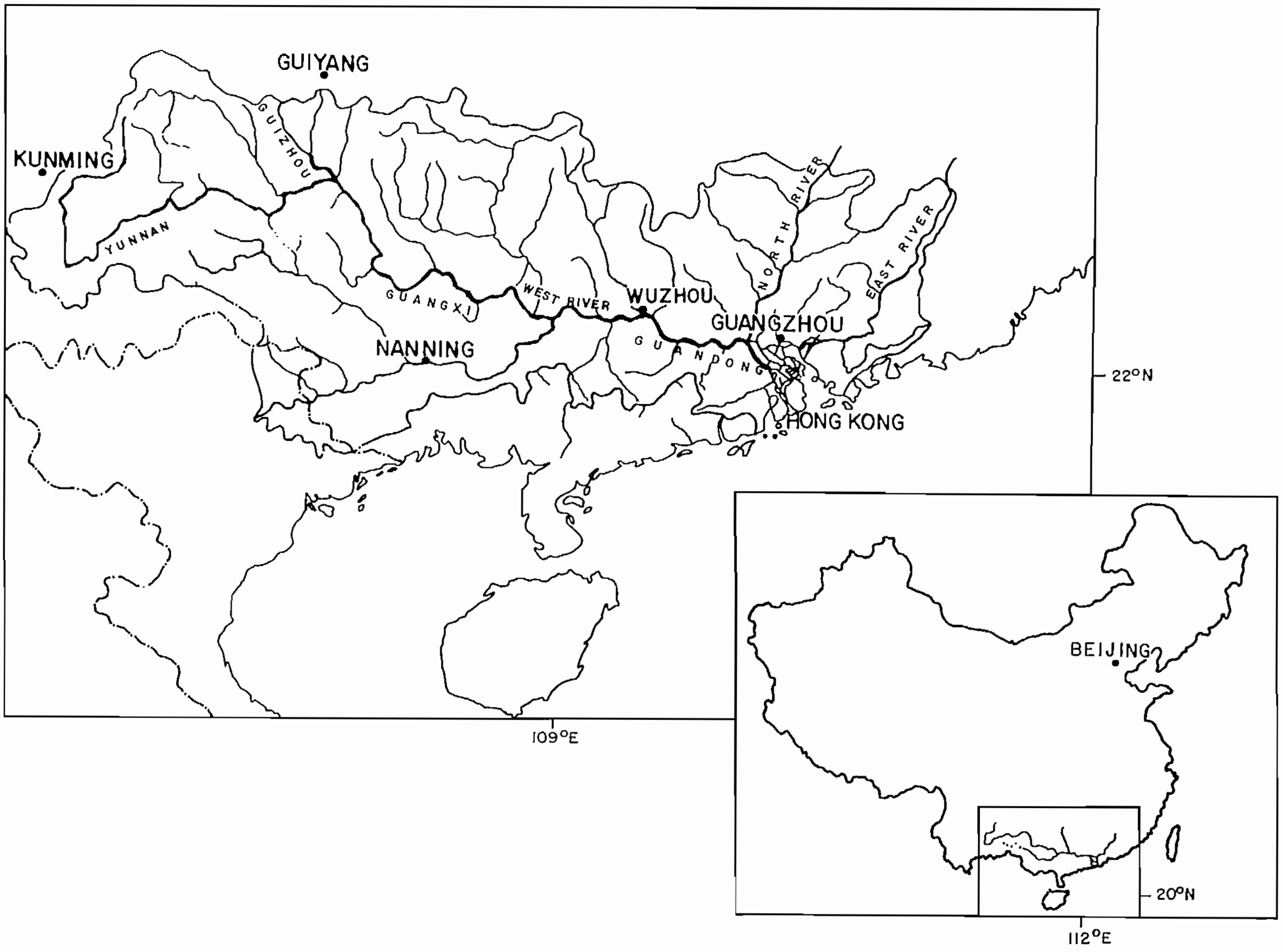

FIG. 1. Location of the Pearl River in China.

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[1] The nine research institutions and universities are: Pearl River Fisheries Research Institute, Fisheries Research Institute of Guangxi Zhuang Autonomous Region, Fisheries Research Institute of Yunnan Province, Fisheries Research Institute of Guizhou

The pH ranged from 6.5 to 8.5 and was higher in the upper reaches of the river than in the lower reaches. The water chemistry is carbonate/bicarbonate dominated and total alkalinity ranged from 75 to 150 $mg \cdot L^{-1}$ in fresh water. Chemical Oxygen Demand (COD) was rather low (0.88–3.23 $mg \cdot L^{-1}$), because of the low organic content of the water and the heavy rainfall.

Of the various nutrients, silicate was the most abundant (0.7–32.8 $mg \cdot L^{-1}$). Nitrate (NO_3-N) and ammonia (NH_4-N) content was relatively high, ranging from 0.1 to 0.5 $mg \cdot L^{-1}$ and <0.1 $mg \cdot L^{-1}$, respectively. Nitrates (NO_2-N) were the lowest at only 0.01 $mg \cdot L^{-1}$. Total nitrogen content had a wide range from 0.04 to 8.29 $mg \cdot L^{-1}$. Phosphate content was not high (0.05–0.1 $mg \cdot L^{-1}$). The total iron content ranged from 0.024 to 0.98 $mg \cdot L^{-1}$.

The results of the physical and chemical analyses showed that dissolved oxygen, pH and the major nutrients were suitable for the growth and reproduction of forage organisms and fish in the Pearl River.

TABLE 1. The physical and chemical characteristics of the Pearl River (1980–83).

Water temperature (°C)	6.5–34.0
Secchi depth (m)	0.02–4.50
Dissolved oxygen ($mg \cdot L^{-1}$)	5.0–7.0
pH	6.5–8.6
Alkalinity ($mg \cdot L^{-1}$)	75–150
Total hardness ($mg \cdot L^{-1}$)	70–140
COD (Mn) ($mg \cdot L^{-1}$)	0.88–3.23
SiO_2 ($mg \cdot L^{-1}$)	0.70–32.8
NO_3-N ($mg \cdot L^{-1}$)	0.10–0.50
NO_2-N ($mg \cdot L^{-1}$)	0.01
NH_4-N ($mg \cdot L^{-1}$)	<0.10
Total N ($mg \cdot L^{-1}$)	0.04–0.29
Total P ($mg \cdot L^{-1}$)	0.05–0.10
Fe ($mg \cdot L^{-1}$)	0.02–0.98

Aquatic Life

Phytoplankton

About 219 genera of phytoplankton organisms belonging to 9 phyla, 12 classes, 26 orders, and 72 families have been identified from 15 streams including main channels and tributaries. More than 90 % of the total number of genera identified belonged to Chlorophyta, Bacillariophyta, and Cyanophyta, while less than 10 % belonged to Xanthophyta, Euglenophyta, Chrysophyta, Pyrrhophyta, Rhodophyta, and Cryptophyta. The highest number of genera were in Chlorophyta, but the phytoplankton of the Pearl River was dominated by Bacillariophyta including *Melosira, Cyclotella, Fragilaria, Gomphonema, Cocconeis, Cymbella*, and *Navicula*; by Chlorophyta including *Chlamydomonas, Chlorella, Chlorococum, Pediastrum, Scenedesmus*, and *Spirogyra*, and by Cyanophyta including *Oscillatoria*.

The mean number of phytoplankters was 330 000 individuals$\cdot L^{-1}$ and mean biomass was 0.565 $mg \cdot L^{-1}$ in 1981 while the mean number was 539 500 individuals$\cdot L^{-1}$ and mean biomass was 0.952 $mg \cdot L^{-1}$ in 1982. The mean number of phytoplankton was 434 700 individuals$\cdot L^{-1}$ and mean biomass was 0.801 $mg \cdot L^{-1}$ over the 2 years.

Bacillariophyta contributed 80.75 % of the total phytoplankton biomass. Chlorophyta, Pyrrhophyta, Euglenophyta, Cryptophyta, Cyanophyta, contributed 8.02, 4.51, 3.71, 2.79, 0.69, 0.38, and 0.06 %, respectively.

Zooplankton

In the Pearl R. zooplankton of 168 genera and 410 species from 3 phyla, 4 classes, 18 orders, and 64 families. Of these, Protozoa included 105 species, Rotifera 124 species, Cladocera 84 species, and Copepoda 97 species.

The mean biomass of zooplankton in the Pearl River was 0.433 $mg \cdot L^{-1}$ with Rotifera, Copepoda, Cladocera, and Protozoa contributing 37.3, 27.9, 25.3, and 9.5 %, respectively.

Seasonal changes of zooplankton were observed in the river. In general, the biomass of Protozoa and Rotifera was greater during the flood season (summer and autumn) than in the dry season (winter and spring) while the inverse was true for Cladocera and Copepoda. The relative biomass of zooplankton in the dry season was greater than that during the flood season (Table 2).

Benthos

The benthic community of the Pearl River was diverse with 5 phyla, 10 classes, and 268 species. More than 70 % of total species identified were aquatic insects. Gastropoda and Lamellibranchia, while less than 30 % of the total number of species, belonged to Crustacea, Oligochaeta, Hirudinea, Polychaeta, Turbellaria, and Numertinea.

The benthos of the Pearl River is dominated by Arthropoda, which contributed 56.13 % of the total species. Of these, aquatic insects accounted for 46.1 %. Mollusca contributed 30.48 % of the total number of benthic species, while Gastropoda and Lamellibranchia accounted for 61 and 39 %, respectively.

The numbers and biomass of benthic organisms differed with section of river. The mean annual number of organisms was 422.5 individuals$\cdot m^{-2}$ and mean biomass was 84.3 $g \cdot m^{-2}$ in 1981–82 in the Guangdong section (lower reaches) while in the Guangxi section (middle reaches), the number of organisms was 1 102–1 319 individuals$\cdot m^{-2}$, and mean biomass was 20.9–21.5 $g \cdot m^{-2}$.

Aquatic Plants

About 132 species of aquatic plants were identified from the river. These belonged to 42 families and 78 genera and included 29 species of floating plants, 41 species of submerged plants and 62 species of emergent plants. Main species are *Marsilea quadrifolia, Salvinia natans, Azolla imbricata, Alternanthera philoxeroides, Myriophyllum*

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[2] This paper was written mainly in accordance with the manuscript of the Report on the surveys of fisheries resources in the Pearl River compiled by the Pearl River Fisheries Resources Survey Commission in 1985.

TABLE 2. Major species of commercially valuable fish in the Pearl River.

Family	Species	English Name
Clupeidae	*Macrura reevesii*	Chinese shad
	Clupanodon thrissa	Gizzard shad
	Coilia mystus	Anchovy
	C. grayi	Anchovy
	Salanx sp.	White fish
Anguillidae	*Anguilla japonica*	Japanese eel
	A. mauritiana	Spotted eel
Cyprinidae	*Mylopharyngodon piceus*	Black carp
	Ctenopharyngodon idella	Grass carp
	Elopichthys bambusa	False salmon
	Ochetobius elongatus	Tube fish
	Squaliobarbus curriculus	Eastern barbel
	Erythroculter pseudobrevicauda	
	E. hypselonotus	
	Hemiculter leucisculus	
	Megalobrama hoffmanni	Guangdong bream
	Parabramis pekinensis	Peking bream
	Anabrilius qiluensis	
	Xenocypris davidi	Yellow tail
	Barbodes caldwelli	Barbel
	B. denticulatus denticulatus	Barbel
	B. denticulatus yunnanensis	Barbel
	Varicorhinus (Onychostoma) gorlachi	
	V. (Onyc.) lini	
	Tor (Foliber) brevibilis brevibilis	
	Sinilabeo decorus decorus	
	Cirrhinus molitorella	Mud carp
	Ptychidio jordani	Mouse fish
	Semilabeo notabilis	Lip fish
	Garra pingi yiliangensis	Ageneiogarra
	Hemibarbus labeo	Bony fish
	H. maculatus	Bony fish
	Saurogobio dabryi	
	Cyprinus carpio haematopterus	Common carp
	Carassius auratus auratus	Crucian carp
	Carassoides cantonensis	Barbelled carp
	Aristichthys nobilis	Big head carp
	Hypophthalmichthys molitrix	Silver carp
Cranoglanididae	*Cranoglanis sinensis*	Cat fish
Siluridae	*Silurus asotus*	Cat fish
Clariidae	*Clarias fuscus*	
Bagridae	*Pseudobagrus fulvidraco*	
	Mystus guttatus	
Ariidae	*Arius sinensis*	
Belontiidae	*Ophicephalus maculatus*	Snake fish
Mugilidae	*Mugil cephalus*	Grey mullet
Serranidae	*Lateolabrax japonicus*	Perch
	Siniperca knerii	Mandarin fish
Sparidae	*Sparus latus*	
Sciaenidae	*Collichthys lucidus*	
Gobiidae	*Parapocryptes serperaster*	
Periophthalmidae	*Periophthalmus cantonensis*	
Cynoglossidae	*Cynoglossus trigrammus*	Sole

spicatum, Potamogeton diatinetus, P. malaianus, P. pectinatus, P. crispus, Najas japonica, Sagittaria pygmaea, Hydrilla verticillata, Zizania latifolia, Echinochloa crus-galli, Lemna minor, Spirodela polyrhiza, Monocharia vaginalis, and *Eichhornia crassipes*.

Fish Composition and Their Distribution

From the system, 381 species of fish including 262 species of freshwater fish and 119 species of brackish-water and diadromous fish have been recorded. Of this, 100 species were commercially valuable with 53 species (mostly Cyprinidae) highly valued (Table 3). The freshwater fish community is particularly diverse, including 262 species representing 18 families (Table 4). The ichthyofauna was dominated by Cypriniformes, including Cyprinidae, Cobitidae, and Homalopteridae and contributed 81.7% of the total number of species (Table 4).

Analyses from four sectors of the Pearl River shows that the number of fish species inhabiting the Guangxi section

TABLE 3. Seasonal changes in the biomass of zooplankton in the Pearl River.

Zooplankton	Floodplain Season		Dry Season	
	Biomass ($mg \cdot L^{-1}$)	%	Biomass ($mg \cdot L^{-1}$)	%
Protozoa	0.047	9.7	0.047	4.9
Rotifera	0.156	32.3	1.120	12.5
Cladocera	0.023	4.8	0.409	42.6
Copepoda	0.257	53.2	0.384	40.0
Total	0.483	100.0	0.960	100.0

(209 species) were more than those in the Guangdong section (161 species), Yunnan section (115 species), and Guizhou section (95 species).

Since the Pearl River is located in the subtropics and the northern tropics, the fish community is not only diverse, but also contains many tropical and subtropical species. Cyprinidae contributed 62.6 % of the total number of species, and is dominated by the Barbinae which, with 50 species, accounted for 30.5 % of the total number of species (Table 4). Six species of barb were particularly common, *Barbodes denticulatus yunnanensis*, *B. lacustris*, *Sinocyclocheilus guilinensis*, *S. grahami yangzongensis*, and *S. grahami tingi*.

Ptychidio jordani and *P. macrops* are endemic to the Pearl River and were highly valuable commercially. Other species of Cyprinidae, such as *Carassoides cantonensis*, *Erythroculter pseudobrevicauda*, and nine species of the genus *Anabarilius* are also endemic. Peking bream (*Parabramis pekinensis*), Guangdong bream (*Megalobrama hoffmanni*), eastern barbel (*Squaliobarbus curriculus*), false salmon (*Elopichthys bambusa*), and yellow tail (*Xenocypris argentae*) have a much wider distribution, and grass carp, black carp, silver carp, mud carp, and common carp are well known as major cultivated fish in ponds.

Estuarine forms were represented by 151 species (16 orders, 52 families and 14 genera). They were dominated by Perciformes (63 species) and Clupeiformes (17 species), some of which had large populations and formed the basis for fisheries in the estuary of the Pearl River. Although there are 27 species of Gobiidae, only two species *Odontamblyopus rubicundus* and *Taenioides anguillaris* were significant in the catch.

The major diadromous fishes include the anadromous Chinese sturgeon (*Acipenser sinensis*), Chinese shad (*Macrura reevesi*), *Clupanodon thrissa* and *Cynoglossus trigrammus*, the catadromous Japanese eel (*Anguilla japonica*), and spotted eel (*Anguilla mauritiana*).

TABLE 4. Freshwater fish of the Pearl River.

Order	Family	Sub-Family	Genus	Species	
				No.	%
Cyrpiniformes	Cyprinidae	Leuciscinae	14	14	5.3
		Abramidinae	11	34	13
		Xenocyprininae	3	4	1.5
		Acheilognathinae	6	12	4.6
		Barbinae	18	50	19.1
		Gobinae	10	26	9.9
		Schizothoracinae	1	5	1.9
		Cyprininae	4	14	5.3
		Hypophthalmichthyinae	2	2	0.8
		Gobiobotiinae	1	3	1.2
	Cobitididae		9	28	10.7
	Homalopteridae		11	22	8.4
SUB-TOTAL			90	214	81.7
Siluriformes	Siluridae		1	6	2.3
	Cranoglanididae		1	1	0.4
	Clariidae		1	1	0.4
	Sisoridae		3	4	1.5
	Amblycipitidae		1	1	0.4
	Bagridae		4	11	4.2
Cyprinodontiformes	Cyprinodontidae		1	1	0.4
	Poeciliidae		1	1	0.4
Symbranchiformes	Synbranchidae		1	1	0.4
Perciformes	Serranidae		1	7	2.7
	Eleotridae		3	3	1.1
	Gobiidae		2	4	1.5
	Anabantidae		2	2	0.8
	Ophiocephalidae		2	3	1.1
	Mastacembelidae		1	2	0.8
TOTAL			115	262	100

Fishery and Dynamics of Fish Stocks

The Guangdong and Guangxi sections of the Pearl River were the major locations of commercial fisheries. In 1982, the annual catch in the Guangdong section was 8 308.5 t (72.4 % of total), compared with 3 174.9 t (27.6 % of total) in the Guangxi section. There were 27 158 fishermen and 9 847 fishing boats in the Guangdong section and 23 421 fishermen and 3 413 boats in the Guangxi section (Fig. 2).

Analyses of catch in different years (1957–64 and 1974–82) show that the mean annual yield was highest in the 1950's (10 367 t). Since the 1960's, there have been dramatic changes in fish yield annually and, although the catch increased somewhat in 1982, the mean annual yield in the early 1980's was only 6 463.7 t, representing a decline to only 37.7 % of the late 1950's catch (Fig. 3).

This decline can be verified by evaluating catches of some commercially valuable species. Annual catches of Chinese shad at the Dongta spawning ground located in the Guangxi section decreased from about 550 t in the 1950's, to approximately 77 t in 1962, and in 1978 declined sharply to only 50 kg.

The lip fish (*Semilabeo notabilis*) was a commercially valuable fish in the North River tributary of the Pearl River, whose mean annual yield declined from 60–70 t in 1956–65 to 17.5–37.5 t in 1966–75, and then to 6.5–7.5 t in 1976–82. Annual catches of the fox goby (*Odontamblyopus rubicundus*), a valued fish in the Pearl River estuary, was 2 420.4 t in 1963, 1 346.1 t in 1961–70, but only 14.4 t in 1981–82 at the Zhuhai city.

The West River, which is one of the main stems of the Pearl River, is one of the most important areas for producing fry of Chinese carp in China. The highest annual yield of fry was 24 billion individuals in 1961. However, fry production has declined year by year since the 1970's. In the early 1980's, catches of fry dropped to their lowest levels; the mean annual yield was 3.55 billion individuals, a decrease to 15 % of the average for the 1960's.

Effect of Human Activities on the Dynamics of Fish Stocks

Overexploitation

Fishing intensity has increased with a trend toward the elimination of the older fish from catches. Although fish yield has declined steadily since the 1960's, fishing intensity is still increasing. The number of fishing boats in the Guangdong section increased from 7 156 in 1975 to 9 843 in 1982. Of these, the number of motor boats increased from 148 in 1975 to 2 742 in 1982. Changes in fishing gear and technology has greatly increased fishing efficiency. For example, since the 1960's coarse cotton gillnets have been replaced by multifilament nylon twine.

The presence of young fish in catches was very common. For example, fingerlings of common carp and *Barbodes caldwelli* contributed 85.7–95.5 % of the total catch in the Guizhou section, and older fish made only up to 2 % of the total. Of the 13 species of commercially valuable fish caught in the Guangxi section, there are more than 10 species in which fingerlings contributed 50 % of the total catch. It is evident that the increasing fishing intensity has severely reduced the number of spawners in the fish population.

Overfishing of spawning grounds is a severe problem. Because of lack of fishery management, a great number of brood fish of some commercially valuable species have been heavily caught by fishermen and nearby farmers. Chinese shad, whose large size and abundance made it a particularly valuable commercial species, seems to be most sensitive to overfishing on the spawning grounds because of its ease of capture, and now contributes only a small proportion to the catches, thus losing its fishery significance in the West River. In the same river, more than 6 000 kg of spawning individuals of Guangdong bream (*Megalobrama hoffmanni*) were caught within five hours by approximately 100 fishing boats during spawning season on the Zhangpitang spawning ground of the Guangdong section (West River).

Fry and Fingerlings are Caught Indiscriminately by Small Mesh Nets

As a result of using gillnets with mesh of only 1.0–1.5 cm a great number of fry and fingerlings have been killed. Each year the average catch of individual fishermen is 54 kg of valuable fry and fingerlings weighing between 5 and 20 g each. In the North River, small mesh nets (2–3 cm mesh) catch 20–50 kg of fry and fingerlings per net. In the Pearl River delta, in August and September, fixed small mesh nets up to 500 m long are used to catch fry and fingerlings with catch rates of about 133 000 individuals per net.

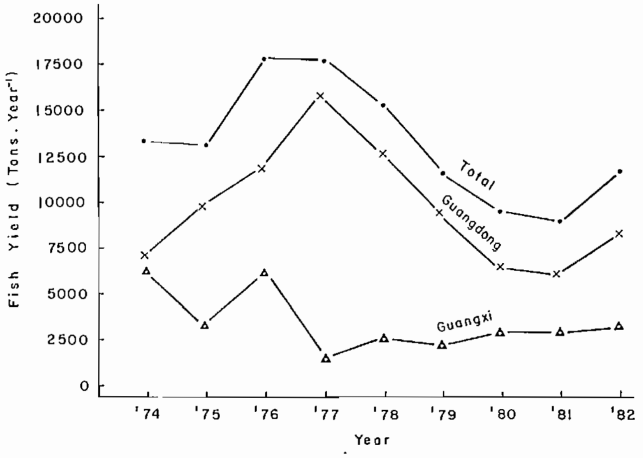

FIG. 2. Estimated fish yield per year (1974–82) from two major sections of the Pearl River.

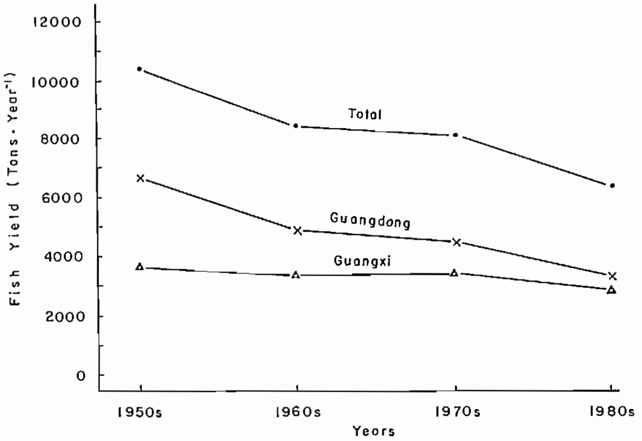

FIG. 3. Fish yield from two major sections of the Pearl R. over a 40-yr period (1950–80).

Fishing by Electric Shocking, Explosives and Poisoning

Fishing by electric shocking, explosives and poisoning are common in the Pearl River, especially in the tributaries. The widespread use of pesticides, quick lime and teaseed-cake kill both large and small fish in great numbers and results in a noticeable reduction of native fish stocks. Electric shocking is harmful to native fish stocks, especially to catfish (Siluriformes) such as *Mystus guttatus* and *Psuedobagrus fulvidraco*.

Effect of Water Conservancy Projects on Fish Stocks

A total of 3 311 different kinds of dams have been built on the Pearl River and its tributaries in the past 30 yr. Most were built without fishways and thus have caused noticeable reductions in the number of certain valuable species because migratory pathways were blocked and spawning areas covered by standing water. For example, after the 1958 construction of the Sijin hydroelectric station on the middle reaches of the Pearl River, a combination of hindrance to migration, reduction in river flow and lowered water temperatures considerably reduced the number of juvenile Chinese carp downstream (Liao 1980).

Damming also produced widespread changes in the dynamics of fish communities in the East River. In the 1960's, there was a great number of migratory fish such as Chinese shad and *Clupanodon thrissa* which moved to the upper reaches of the East River each year. During the summer, a great number of these migratory fish were caught by fishermen. Although only fragmentary data are available, in one instance two fishing boats caught 2.5 t of *Clupanodon thrissa* each year. However, migratory pathways were blocked following the construction of five dams in the lower reaches and many reservoirs in the upper reaches of the river. The migratory fish, including Chinese shad and *Clupanodon thrissa* virtually disappeared from the river by 1970. While in the 1950's, a great number of fry of Chinese carps, especially mud carp, were caught, and the output was 200 million individuals each year, by 1986 the fry production was so low as to have lost any significance to the economy of the river.

Effect of Water Pollution on Fish Stocks

Following the development of mining and smelting industries along the Pearl River, sources of contamination and water pollution became serious. Increasing quantities of waste water from factories were discharged directly into the rivers. Approximately 1 230 000 t of untreated industrial wastewater is discharged directly into the streams of the Guangxi sector each year. Some streams have suffered such severe contamination from industrial effluents that native fish stocks have become adversely affected. Pollution in the North River is serious, with widespread degradation of water quality and regular fish kills caused by untreated industrial waste water.

Use of various pesticides for agriculture is expected to increase rapidly. After rainfall, a great quantity of pesticides is washed from paddy fields into rivers causing serious pesticide pollution. Analysis of water quality shows, for instance, that the benzene hexachloride (BHC) content in the Pearl River delta exceeds the maximum allowable concentration established by the State legislation. A great number of fish, especially fry and fingerlings, have been killed by serious pesticide pollution in some streams.

Strategies for Rehabilitation and Conservation of Fishery Resources

The Pearl River is well-suited for the production of commercially valuable fish because of its richness and variety of forage organisms, fish species diversity and favourable ecological conditions. However, unless a strong effort is made to strengthen fishery management, regulate exploitation and prevent further deterioration of the aquatic environment, the future is precarious. A comprehensive ecosystems rehabilitation strategy must be designed with effective measures to alleviate the key stresses affecting the aquatic ecosystem of the river.

Management of the fishery

a) Strict Limitation on Fishing for Valuable Fish Species

It is obvious that some larger migratory species, such as Chinese shad in the West River have declined because of increasing fishing intensity in the estuary of the Pearl River. Effective measures to alleviate the fishing pressure and reduce fishing intensity in the river are needed. As a first step, the number of fishing boats should not increase. The fishery authorities should stop licensing any new built boats until the river fish stocks are rehabilitated. It is also necessary to prevent fishermen from coastal water fishing in the river.

b) Closed Seasons and Closed Fishing Grounds

Seasons and areas closed to fishing are necessary to allow fish to reproduce undisturbed and for the young to grow to a reasonable size before they are exposed to the fishery. Catching migratory fish such as Chinese shad and Chinese sturgeon should be prohibited during their migration to the spawning grounds.

c) Mesh Regulation

The use of small mesh gear, such as gillnets and fixed nets, to catch juveniles and fingerlings of valuable fish in rivers is very common. As mesh size is reduced to catch smaller fish, the larger ones inevitably tend to decline, and disappear. There is, therefore, an urgent need to limit mesh size of major gear, such as gillnets, trammel nets, and prohibit use of small fishing gear.

Liao et al. (1986) suggested that the mesh size of gillnets for catching mouse fish (*Ptychidio jordani*) should be enlarged to 6.6 cm and the use of nets of less than 5 cm mesh prohibited.

Chen (1985) gives a detailed analysis of the relationship between the catchable size of river fish and mesh size of gillnets. He notes that mesh size of gillnets is closely related to body length and weight of fish in the Pearl River. Two formulae may be applied as follows:

$A = K_1 L$

$A = K_2 \sqrt[3]{G}$

where A is the length of mesh (mm), L is the body length (mm), and G is the body weight (g), K_1 is the coefficient of bodily form, and K^2 is the coefficient of condition.

d) Banning Harmful Gear and Methods

The restriction of more destructive fishing practices is most important for the rehabilitation and conservation of fish stocks in rivers. Harmful fishing gear and methods, such as electric shocking, explosives and poisoning have an adverse effect on the native fish stocks and should be prohibited.

Management of The Riverine Environment

a) Control of Water Pollution

Because of increasing problems with environmental pollution which have further reduced the quality and quantity of some commercially valuable fish in the Pearl River, it is most important to control and to eliminate gradually the discharge of hazardous substances into the river ecosystem.

Analyses show that although the Pearl River system is generally only lightly polluted, the situation in some tributaries and reaches is more serious. Widespread degradation of water quality is detected, particularly in some streams of the delta, near cities where industrial effluents are discharged. Here environmental deterioration has progressed to the point where many elements of the fish fauna have been lost.

Fishery authorities should collaborate with the Department of Environmental Protection to take effective measures to maintain an acceptable water quality and prevent further deterioration of the aquatic environment. The Fisheries Law of the People's Republic of China (1986) stipulated that all those who use certain harmful fishing gear and methods for catching valuable fish be fined, their fish gear confiscated, and their fishing licences cancelled. Factories discharging untreated industrial wastes directly into rivers should be held responsible for any resulting accident or fish kill and should be made to compensate for the economical losses. The agricultural authorities should likewise impose restrictions on the use of pesticides in paddy fields in order to prevent pesticide pollution in rivers.

b) Fish Passes

Fishways or other types of fish passes are not incorporated into most dams now built on rivers. The lack of such structures has played an important role in the reduction of fish production. This situation should be remedied by the construction of fish ladders at dams, artificial propagation of brood fish whose migration is blocked by dams and by stocking fingerlings in the river. Such remedies have been successful in the restoration of American shad in the Susquehanna River (Howey 1981). More than 20 dam fishways on streams in Jiangsu Province, Eastern China, have proved successful in facilitating fish migration (Nanjing Water Conservancy Research Institute et al. 1982). Water conservation authorities should ensure that fish passages are incorporated into new dams wherever justified.

c) Stocking

Stocking of ayu (*Plecoglossus altivelis*) into the rivers of Japan has a history of more than 60 yr, and plays an important role increasing the fish yield in Japanese rivers (Ishida 1976). Some streams of the Pearl River delta have been stocked since 1979. The results so far have been encouraging. For instance, between 1980 and 1984 the Tanjiang River, a 90-km long distributary of the Pearl River delta was stocked with 47 100 000 fingerlings, including common carp (63.4 %), bream (20.4 %), black carp (9.4 %), big head carp (3.9 %), grass carp (1.3 %), silver carp (1.2 %), and *Labeo rohita* (0.3 %) (an average of 9 420 000 fish stocked annually). A noticeable increase in fish yield was observed within 5 yr, with the catch reaching 1 503 t in 1984, twice that of 1980 (Bureau of Sinhui County 1984). Results show that stocking may be an effective measure for restoration of river fisheries in China. This must be accompanied by other fishery management measures, especially a ban on catching fry and fingerlings by small mesh nets.

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References

CHEN, F. B. 1985. Catchable size of river fish and mesh size of gillnets. Sci. Technol. Fish. 2: 44–47.

FISHERIES BUREAU OF SINHUI COUNTY. 1984. Proliferation of fisheries resources and development of river fishery. Sci. Technol. Fish. (Spec. Issue for Aquaculture) 1: 43–44.

HOWEY, R. G. 1981. A review of American shad restoration efforts on the Susqehanna River. Lamar Info. Leafl. No. 81-04: 1–5.

ISHIDA, R. 1976. Stocking of Ayu (*Plecoglossus allivelis*) in the river of Japan. FAO Tech. Conf. Aquaculture. FIR:AQ/Conf/76/E.50.

LIAO, G. Z. 1980. Preliminary approach to the water conservancy project and the "rescue of fish". Freshw. Fish. 1: 1–4.

LIAO, G. Z., B. Z. YOU, Y. Q. BAI, D. F. GAO, D. F. LIU, S. M. LIANG, AND, S. X. PANG. 1986. Age, growth, feeding habits and reproduction of the mouse fish (*Ptychidio jordani*) in the Pearl River, China. J. Fish. China 10(1): 71–86.

NANJING WATER CONSERVANCY RESEARCH INSTITUTE, AND FRESHWATER FISHERIES RESEARCH INSTITUTE OF JIANGSU PROVINCE. 1982. Fish Way. Electric Industry Press, p. 131–162.

FISHERIES BUREAU OF GUANGDONG PROVINCE. 1986. Handbook of Chinese Fisheries Law, p. 1–8.

Dynamics of Fish Assemblages in River Systems — a Synthesis

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Abstract

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The comprehensive review of a diverse set of global river systems during the LARS Symposium generated many new insights, some at the level of innovative concepts or even first principles. The areas of concern where greatest progress was made included those of seasonality, predictability, nutrient availability, assemblage complexity, fish production, oceanic dependency, nature of regulations, and human impact. For each of these subjects, the knowledge base was increased markedly. In addition, the understanding of river–landscape interactions was advanced a step beyond that of the River Continuum Concept (RCC), although the latter was deemed to be an appropriate first approximation model for subsequent revision according to local variability. The RCC, however, was often inadequate in describing events in the potamonic lower reaches of rivers, and alternative concepts such as the River Pulse concept have to be invoked in those high stream orders. Preliminary information suggests a three-dimensional structure to river–floodplain processes, but reliable generalizations cannot yet be made.

Alternative methods suitable for application in the interim, are simple heuristic models of river fisheries yields as a function of environmental variables as often used in lakes. These models proffer an increased understanding of a complex, multidimensional, ecosystem for large rivers. On a practical basis, they may provide a rapid first approximation of the potential of a river to produce fish, and beyond this level, point the way to further refinement for future investigators. As long-term data sets become available, the value of these models will be determined with greater certainty. Fish assemblages in large rivers throughout the world appear to behave in a similar manner in response to externally imposed biotic and abiotic stresses. Current understanding of large rivers is limited by the relatively little knowledge available for these extremely complex systems and to improve this, collaboration by workers in many disciplines is essential.

Résumé

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L'examen approfondi d'un ensemble mondial diversifié de réseaux hydrographiques réalisé pendant le Symposium international sur les grands cours d'eau a permis de faire bon nombre de percées se présentant sous la forme de concepts innovateurs ou, même, de principes fondamentaux. Les domaines d'intérêt où les progrès les plus importants ont été accomplis sont ceux de la saisonnalité, de la prédicabilité, de la disponibilité des matières nutritives, de la complexité des assemblages, de la production de poisson, de la dépendance océanique, de la nature des régulations et des incidences anthropiques. Nos connaissances de chacun de ces sujets ont pu être accrues de façon marquée. De plus, la compréhension des interactions entre les cours d'eau et le milieu physique a suffisamment progressé pour dépasser le stade du concept de l'élément de continuum des cours d'eau, concept par ailleurs considéré comme un premier modèle d'approximation approprié pour l'apport de corrections en fonction de la variabilité locale. Le concept du continuum s'avérait cependant souvent insuffisant pour décrire les événements des sections potamiques des cours d'eau et d'autres concepts, tels celui des impulsions, devaient être appliqués à ces cours d'eau d'ordre élevé. L'information préliminaire disponible porte à croire à l'existence de processus d'interaction cours d'eau-plaine inondable à structure tridimensionnelle, mais il est encore trop tôt pour formuler des généralisations fiables.

Les méthodes pouvant être appliquées actuellement sont représentées par de simples modèles heuristiques du rendement des pêches des cours d'eau en fonction de variables environnementales, tels ceux qu'on applique souvent aux lacs. Ces modèles offrent la possibilité de mieux comprendre l'écosystème multidimensionnel complexe des grands cours d'eau. D'un point de vue pratique, ils peuvent fournir rapidement une première approximation du potentiel d'un cours d'eau à produire du poisson et même indiquer la voie d'un plus grand raffinement aux chercheurs. La valeur de ces modèles pourra être établie avec plus de certitude lorsqu'on disposera de séries de données portant sur de longues périodes. Il semble que les assemblages de poissons des grands cours d'eau du monde entier réagissent de façon semblable à des contraintes biotiques et abiotiques externes. Notre compréhension des grands cours d'eau est actuellement limitée par les connaissances relativement limitées que nous avons de ces systèmes extrêmement complexes et des progrès ne pourront être accomplis dans ce domaine que grâce à la collaboration de chercheurs de disciplines diverses.

Introduction

Knowledge of large rivers and their fisheries has increased rapidly over the past decade after being a relatively neglected backwater of aquatic biology. Until now there has been little systematic review of the topic although earlier symposiums (e.g. Oglesby et al. 1972; Whitton 1975) and more recent compilations (e.g. Davies and Walker 1986) have assembled a considerable amount of information. Most recently, the Large River Symposium (LARS) provided an opportunity not only to review this knowledge but also to synthesize it in an attempt to derive more general principles of river ecology and river ecosystem management.

Papers presented to LARS provided information on 33 rivers across the globe and also reviewed aspects of many others. Initially, the rivers discussed give the impression of very diverse sets of systems although four main groups could be distinguished:

i) Northward flowing Arctic rivers that are generally poor in energy input and whose fish assemblages contain a high proportion of anadromous species [Hudson and James Bay rivers (Roy 1989), Moose River (Brousseau and Goodchild 1989), Mackenzie and Churchill rivers (Bodaly et al. 1989)].

ii) Streams flowing into the Atlantic or Pacific oceans where the dominant commercial fisheries and management strategies are aimed at salmonids [Mirimichi and Exploits rivers (Randall et al. 1989, Fraser River (Northcote and Larkin 1989), Columbia River (Ebel et al. 1989].

iii) Temperate and sub-tropical rivers that have been modified to differing degrees [Colorado River (Carlson and Muth 1989), Missouri River (Hesse et al. 1989), Tennessee River (Voigtlander and Poppe 1989), Mississippi River (Fremling et al. 1989), Hudson River (Limburg et al. 1989), Thames, Trent and Wye rivers (Mann 1989), Volga River (Pavlov and Vilenkin 1989), Vistula River (Backiel and Penczak 1989), Danube River (Bacalbasa-Dobrovici 1989), Rhine River (Lelek 1989), Pearl River (Liao et al. 1989)].

iv) Tropical rivers that are relatively unaltered [Niger River (Malvestuto and Meredith 1989), African rivers (Welcomme 1989), Ganga River (Natarajan 1989), Amazon River (Bayley and Petrere 1989), La Plata System (Quirós and Cuch 1989), Orinoco River (Novoa 1989), Madgalena River (Valderrama and Zarate 1989)], although generally, African rivers tend to be less modified than those of Asia and South America.

Despite these distinctions some more or less consistent latitudinal trends can be discerned when various characteristics of the rivers of the world are considered.

Seasonality — With the possible exception of certain small equatorial streams, all rivers show marked seasonality. This tends to be dominated by two parameters that are the principal abiotic factors affecting fish assemblages; hydrological regime and temperature — i.e. with decreasing latitude the significance of temperature as a limiting factor decreases and the role of the hydrological regime increases.

Predictability — The predictability of annual hydrological regimes is high at both low and high latitudes where seasonality is extremely marked. In the humid temperate zone, more diffuse rainfall patterns introduce more within-year variation.

Nutrient availability — While the nutrient status of small rivers throughout the world varies widely, large river channels tend towards a mediated or average condition whereby the total amount of nutrients is reasonably consistent by region. A trend can be detected where nutrient concentrations as defined by conductivity (K_{25}) or total dissolved solids (T.D.S.), are relatively low at extremely low latitudes as well as extremely high ones. This trend has also been noted by Maybeck (1979) as related to his morphoclimatic types.

Assemblage complexity — Clear relationships emerge when the number of fish species in rivers is compared with the area of their basins (Welcomme 1985). The nature of the relationships from various continents indicates clearly that species diversity declines with increasing latitude in basins of similar size. The tendency for relatively impoverished fish faunas to occur at high latitudes is reinforced by the effects of glaciation.

Fish production — Despite the common contention that tropical waters are more productive than temperate ones there is at present little evidence to substantiate this in the case of rivers (Welcomme 1985). However, the inordinately low productivities cited for the north flowing Arctic streams would indicate the existence of a latitude-dependent effect there. Furthermore, much of the apparent high production of some mid-temperate rivers may come from the supplementation of oceanic resources by anadromous species.

Oceanic dependence — There is a marked tendency for fish assemblages to become more dominated by anadromous species at high latitude. Anadromous and diadromous fishes play a slight role in most tropical systems whereas they dominate the populations of north temperate and Arctic rivers as well as those of Australia, New Zealand, and southern South America. A third class of fishes inhabit estuarine or inshore regions influenced by freshwater plumes and move into the lower reaches of rivers to breed. These species, which are termed semi-anadromous by Eastern European workers, are more evenly distributed.

Nature of regulation — The dynamics of fish assemblages in rivers appear to be regulated mainly by abiotic factors at low and high latitudes, whereas in the intermediate temperate belt the main regulators appear to be biotic. It is, however, likely that in the distant past, abiotic factors regulated the fish assemblages of the temperate zone to the same extent that they do in the tropics today. Because recent human modifications have been aimed at keeping some of the most important of these factors relatively constant, biotic regulatory mechanisms now exercise control. If this supposition is correct, a similar tendency for biotic factors to succeed abiotic ones as the principal regulatory mechanisms should be followed as tropical and Arctic rivers become increasingly controlled.

Human impact — The degree of modification of river systems is at present maximal in the intermediate climatic zone and lessens towards the Arctic and the equator. However, present trends towards the construction of large dams on many of the tropical river systems may alter this pattern in the future.

The need for simple models and guidelines for management has led to the formulation of a number of simplistic models. These have been designed either to provide a generalized conceptual framework for understanding the aquatic ecosystem or to provide the crude estimates of potential yield required for the early stages of decision making. Such simple heuristic and conceptual models frequently sacrifice precision for rapidity of solution to questions, and are open to criticism in that individual rivers often do not conform to their predictions. However, study of the reasons why any particular system deviates from the behaviour of other members of a set can shed light on its nature and eventually lead to an improved general model. The Synthesis Group on Community Dynamics considered existing models to determine their validity in light of the material presented at the Symposium and investigated ways in which they might be modified. Three main groups of models were available for consideration and were discussed: River–landscape interactions which arise out of the River Continuum Concept (Vannote et al 1980); predictive algorithms for catch as a correlate of some morphological or edaphic variable resulting in models congruent to the Morphoedaphic Index as applied to lakes (Ryder et al. 1974), or rivers (Welcomme 1976); and concepts of responses of fish assemblages to human-induced stresses (Rapport et al. 1985).

River-Landscape Interactions

Many workers have noted the apparent ecological succession associated with changes in morphology along a river. The River Continuum Concept (RCC) was formulated by Vannote et al. (1980) in an attempt to provide a coherent description of the various morphological and biological changes which occur during progression downstream from small streams to large rivers. The RCC considers the entire fluvial system as a continuously integrated series of physical gradients and associated biotic adjustments. River systems are envisioned as longitudinally linked systems in which ecosystem level processes in downstream reaches are conditioned by other processes occurring further upstream. This concept has provided a useful generalization about the source, relative magnitude, and temporal and spatial variation of the organic matter supply, as well as about resource partitioning along the length of the river (Minshall et al. 1985).

Welcomme (1985) pointed out that the ecological changes projected by the RCC are mostly realized within low order streams and little further change is predicted in rivers higher than order 6. Thus, the RCC may be a useful descriptor for changes occurring in the first 200 km or so of a river system, that is, including the transition from rhithron to potamon. However, once the potamonic phase is reached, conditions remain more stable for the remainder of the river's course, often for several thousand kilometres. The number of ecosystem forcing functions as well as the structural complexity of fluvial ecosystems tend to increase downstream. As a consequence, both maximum species diversity and maximum fish biomass are to be found on, or associated with the downstream floodplains, which are the areas least sensitive to the predictions of the RCC.

Only a few studies have attempted to interpret the RCC in terms of river metabolism and fisheries. Naiman et al. (1988) found considerable biological predictability in system metabolism and carbon inputs for the 20 000 km^2, sub-arctic Moisie River in Quebec, Canada. This river, with a 9th order mainstem of less than 100 km and a negligible floodplain, but with numerous bogs and lakes in its basin, follows the predictions of the RCC. Within this basin fish biomass and production are greatest where organic carbon processing efficiencies are highest. Quirós and Baigun (1985) also found a similar correlation between the quantity of organic nitrogen and carbon in the water column, and the biomass and catch per unit effort of the fish stock in the subtropical Paraná River of Latin America. Here, island lagoons under great influence of water from the main channel, contained less fish biomass than those near the margins of the floodplain which were influenced by organically rich secondary channels and lateral tributaries. Quirós and Cuch (1989) found that there was a longitudinal increase in nutrients, zooplankton, benthos, fish and organic matter in both the water column, and the sediments of the main channel of the Paraná. The Paraná River therefore, appears to be spatially structured along its main axis, although this does not agree in totality with the predictions of the River Continuum Concept, because it has a second axis across the floodplain, perpendicular to the first.

While these studies are encouraging, we propose that productivity in large river floodplains is controlled by so many factors that it is not possible to derive precise, universal fish yield estimators for physiographic reaches along a river–floodplain system. A more specific approach to estimating fish yields is required based on river–floodplain ecosystem dynamics.

Possibly such studies should be based on a hierarchical classification of large river basins (*sensu* Frissel et al 1986). Such spatial-temporal hierarchies can be applied at the level of a homogeneous river reach (Mollard 1973; Kellerhals and Church 1989) and separated into units which align on three dimensions of the river–floodplain system: namely, the longitudinal continuum of geomorphic patterns and ecological functions, the lateral spread of aquatic, semiaquatic and terrestrial ecosystems on the floodplain, and the vertical dimension represented by the groundwater system (Roux et al. 1982; Amoros et al. 1986; Ward and Stanford 1989). Functional units of the river–floodplain landscape include the main channel or channels of the river, backwaters still connected to the channel downstream, floodplain water bodies arising from a variety of hydrodynamic processes and the plain itself. Functional units must be considered on a temporal continuum since different successions develop on different geomorphological surfaces (Bravard et al. 1986). Using a systematic approach, explanatory and predictive models can be derived to estimate fluvial system functions in the "natural state" and under human impact.

Welcomme (1979) and Junk et al. (1989) have focused on seasonal pulsing of flood flows onto the floodplain as the driving force controlling the river–floodplain complex. As water inundates the floodplain, the floodplain pulse produces a "moving littoral" ecosystem unit which prevents permanent stagnation and allows rapid recycling of nutrients and organic matter (Junk et al. 1989). This results in higher productivity than in systems which are either wet or dry, permanently.

Such models provide concepts which can lead to a more refined view of a river–floodplain system. When coupled with geographic information, systems of differing scales (satellite imagery, high altitude photogrammetry, etc.), the extent of seasonal flooding and of the functional ecological units can be determined, as well as rates of inundation and drying as the flood pulse passes downstream.

These concepts can be used to address both biogeochemical processes and carbon dynamics, as well as biotic assemblages. Most objections to the RCC came from the community and population biology approaches to stream and river systems. An ecosystem approach to a large river basin or reaches of a large basin, diverges from the classical approach by favouring mass balance of carbon or nutrients to help identify areas needing study. These are usually identified as a set of ecosystem metabolic ratios (P/B or P/R) which are used to compare stream and river processes in different geographic regions. The key role of chemistry as the principal interface has been recognized by all disciplines, providing a common language for communication and for coordinated concepts and experiments, although when dealing with particulate or dissolved organic carbon it becomes exceedingly difficult to say where the chemistry ends and the biology begins. This approach has been used at the macroscale of the Earth to examine linkages between continents, oceans, atmosphere, lakes, and rivers (e.g. global carbon cycling as affected by deforestation, agriculture, industrialization, acid rain and the effects of climatic shifts). It applies also at the basin level where the emphasis will be to relate the fluxes of nutrients, carbon, and biotic materials, through the three dimensions of the river–floodplain complex.

Predictive Models for Catch

Despite the difficulties in deriving a rational basis for catch predictors in rivers, a need for an heuristic model indicative of river fish yields has long been recognized by river ecologists who are often tempted to apply suitably modified, extant lake models to river systems (e.g. Welcomme 1979). The latter expressions, sometimes termed morphoedaphic index (MEI) models, are often utilized for making a first approximation estimate of potential fish yields for lakes and reservoirs (Ryder et al. 1974). They are beneficial in this application because of the predictable behaviour of nutrients and energy in biospheric systems. A specific MEI ratio used for lakes includes a quantified nutrient value, or nutrient surrogate, in the numerator of the index (e.g. total dissolved solids or conductivity), and another value for energy dissipation such as mean depth in the denominator, scaled by a dimensionally correct coefficient indicative of latitudinal effects. This ratio varied globally, over a trophic range of lakes, from those with an excess of nutrients to those that are nutrient deficient. The latitudinal coefficient applied to the MEI ratio allows a correction to be made for thermal variation (e.g. Schlesinger and Regier 1982).

Morphoedaphic models for rivers require a different approach because the fundamental trophic relationships are different, that is, they are more dependent upon inputs from the terrestrial system, be it riparian forest or floodplain grassland, as a primary source of energy and nutrients. This means that most of the energy in a river system passes through the detritus phase rather than the phytoplankton, thus the classical trophodynamic pathway usually ascribed to lentic environments (Lindeman 1942) is not applicable to most running waters, *sensu stricto*.

Experience from other types of aquatic systems would suggest that fish production in rivers should be low when nutrient concentrations in them are low (i.e. $K_{25} < 40$ μS as expressed in units of conductivity, Fig. 1). This is true for certain types of aquatic systems such as streams flowing over refractory substrates (e.g. Gibbs 1970), and in the rhithrons of rivers at high and mid-latitudes. Thus, in the many temperate streams, fish production in the rhithron may be nutrient-limited. In the potamon, however, there is as yet no evidence from existing data sets that catch is so limited. This may be because the availability of food for fishes during the flood in rivers whose waters contain more

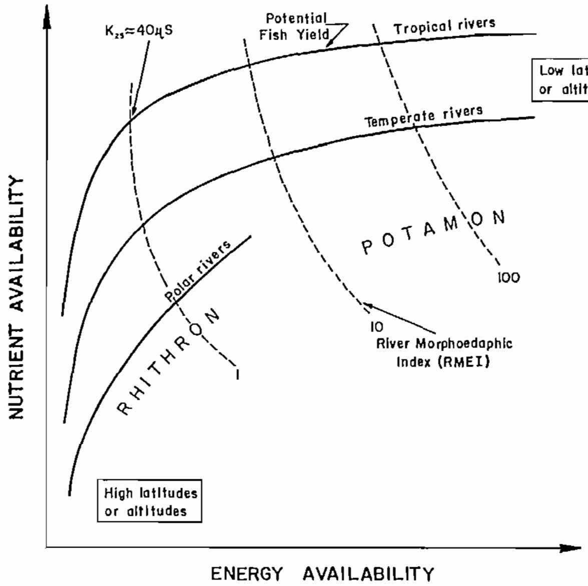

FIG. 1. Theoretical diagram of nutrient availability as a function of energy availability in rivers from different latitudes. Relative fish yields for tropical, temperate, and polar rivers are represented by solid curves while river morphoedaphic indices are shown as broken-line curves. The rhithrons of most river systems usually receive relatively low levels of nutrient and energy inputs, while the potamons of the same river set receive higher inputs. Accordingly, the rhithrons of polar rivers tend to be the least productive globally, on an annual basis, while the potamons of tropical rivers have the highest potential productivities. Tropical river fish yields are most generally limited by energy availability, while polar rivers are nutrient limited.

than a certain threshold quantity of nutrients, exceeds the feeding capacity of the total fish assemblage. Below the threshold, an apparent response to low nutrient concentrations can be detected in catch figures from certain blackwater rivers (e.g. Welcomme 1985). Thus some streams at high latitudes or altitudes tend to be nutrient-dependent for their entire length, while tropical rivers (and possibly unmodified temperate rivers) tend to be morphometrically controlled in terms of their fish production capability (Fig. 1). As high latitude streams have low energy inputs for a large part of the year, and tropical streams are often located on nutrient-deficient, lateritic soils, just the opposite effect might be expected. This seeming thermal-nutrient paradox may be resolved by the nature of the nutrient processes driving the system. In temperate rhithronic streams, nutrient dynamics dependant on processing inefficiencies described by the River Continuum Concept may be dominant. By contrast, nutrient balances in the potamonic floodplain zones may be dependent upon nutrients generated on the floodplain and regulated by the pulse effect.

The morphometric factor in the river morphoedaphic expression (RMEI) therefore, is area rather than mean depth, the latter of which has been used successfully in lakes (Ryder et al. 1974). Depth effects are insignificant in rivers when compared to areal effects because of the low global variance of depth in rivers as compared with the wide variance found in lakes (Ryder and Pesendorfer 1989). Furthermore, variations in area are readily transmitted to fish assemblages both through augmented or decreased living space, albeit temporary, and the different areas available for nutrient inputs.

Perhaps because of the latter effect, variations in traditional edaphic factors are not immediately detectable in rivers where the nutrient base exceeds a fairly low threshold.

In these rivers simple relationships such as those formulated for African rivers by Welcomme (1976) of the form:

$$C = aL^b$$

relating catch (*C*) to the length of the river channel (*L*);

$$C = aA^b$$

relating catch to the drainage basin area (*A*); or

$$C = a + bX$$

where *X* is the total wetted area of the floodplain and *a* and *b* are dimensionally correct coefficients that have been applied successfully to other tropical systems. These general relationships cannot, however, be extended to all other sets of systems, such as tropical rivers poor in nutrients or rivers from other climatic zones. To do this it would be necessary to modify those equations by inserting coefficients to describe edaphic and latitudinal variables. A relationship:

$$R\mathrm{MEI} = XEN$$

may be obtained where *X* would equal the total wetted area of the floodplain (or some correlate of it such as mean wetted perimeter of the main river channel plus its floodplain); *E* would represent a coefficent for latitude representing energetic efficiency, perhaps such as mean annual temperature, and *N* would represent the concentration of the principal limiting nutrient (usually phosphorous in freshwater systems). In this instance, both area (*A*) and river length (*L*) would be considered as close correlates of *X*, and including them both in the equation would reduce its efficiency.

At present, there are insufficient data to establish the precise nature of the relationship between *R*MEI and fish yield, but, because of the types of relationships expressed in Fig. 1, it is highly unlikely that this would be linear. Accordingly, some equation of the form:

$$C = a\ \mathrm{RMEI}^{\mathrm{b}}$$

may be expected to emerge.

Response to Differences in Flood Strength

Because fish production bears a close relationship to the extent of the floodplain, year-to year variations can be anticipated as a result of differences in annual flood strength. Such changes fall into two types: (1) same year effects and, (2) delayed effects.

Same year effects include the very clear inverse correlations that often emerge between the amount of water remaining in the river during the dry season and the catch (see for example Annibal 1983; Vidy 1983) and arise from the different vulnerabilities of fish assemblages to the available fishing effort. Conversely, positive same-year correlations with high water levels have also been described by Novoa (1989) for the Orinoco where a greater number of floodplain lagoons are connected to the main channel during high floods permitting improved migration of the fish resident therein. These different responses reflect the complexities of the hydrological dynamics and structure of river–floodplain systems and the fisheries that exploit them.

Delayed effects are more complex and assume that differences in recruitment, survival and growth resulting from year-to-year differences in flood strength are transmitted to future years. These relationships are usually described by formulae of the form:

$$C_y = a + b(p1\mathrm{HI}_{y-1} + p2HI_{y-2} + pz\mathrm{HI}_{y-n})$$

where C_y = catch in a year; HI = index of flood intensity and *p* = relative importance of a particular year's flood (*p* = 1) and *a* and *b* are regression coefficients. Such effects have been described by several authors including Holčík and Bastl (1977) and Krykhtin (1975) as well as Quirós and Cuch, Novoa, and Welcomme at LARS. Additional information about the fishery may be gained from changes in *p* in sub-regressions within any one data set. Thus the overall regression for 19 years of data from the Central Delta of the Niger (FAO data repository):

$$C_y = 151.73 \log(0.7\ \mathrm{HI}_{y-1} + 0.3\ \mathrm{HI}_{y-2}) - 428.26$$

concealed a change in the catch structure where fishes 6 months old constituted 50 % of the catch in 1974, and where the same age class formed 90 % of the catch in 1984.

It was concluded that regressions based on such effects may be sufficiently precise to be used for predictions for management purposes provided there are enough terms in the data set. It is clear, however, that delayed effects may not be apparent in complex fisheries where the catch includes a large number of species drawn from a great range of age-classes, and where hydrological effects change the vulnerability of fish to capture.

Concepts of Responses to Stress by Fish Assemblages

Types of Stress

Aquatic ecosystems are subjected to a considerable range of stresses including damming and channelization, bunding (creating embankments) and reclamation of the floodplain, water abstractions, contamination with toxic materials, loading with organic matter and nutrients, wood storage and exploitation of living aquatic resources. In addition to these direct interventions on the river, any activity pursued within the drainage basin will also eventually be reflected in some way in the aquatic ecosystem. Each stress invokes a unique response, but it is difficult to assign any particular response by the fish assemblages to a specific stress in large rivers because usually, multiple stresses are acting simultaneously. For example, it has frequently been difficult to judge whether the disappearance of a species from a system could be attributed to environmental change, fishing pressure or even the introduction of a new species. However, there is considerable evidence that some stresses mimic each other in their effects (Rapport et al. 1985) and it may be valid to propose generalized heuristic models of the behaviour of ecosystems under a family of human induced stresses.

Although Rapport et al. (1985) list five families of stresses, current knowledge of the responses by fish assemblages would suggest that these may, in turn be grouped into two main categories — abiotic and biotic.

Abiotic Stresses

The abiotic category groups those structures such as dams or levees that physically modify the aquatic ecosystem. Their intensiveness may best be gauged by the extent to which they alter the environment. Responses by fish assemblages are apt to be discontinuous and centered on groups of species whose biology is affected by the disturbance in the system (Ward and Stanford 1989). Thus obligate anadromous or potamodromous species will tend to disappear in systems where the main channels are blocked by large dams, while floodplain spawners are selected against by channelization or other stream regulation processes which reduce or eliminate the annual flood. Actual changes appear less predictable because of conservatisms which tend to sustain the natural system. For example, no species have been lost from the extensive Missouri–Mississippi river system despite extensive modification (Fremling et al. 1989; Hesse et al. 1989) possibly because this system still retains remnants of its original riverine character. In other extensively modified systems, such as the Pearl (Liao et al. 1989) or the Volga rivers (Pavlov and Vilenkin 1989), the original fauna are still intact or even expanded through immigration or the introduction of new species, but is only maintained in this state through artificial stocking programmes. Other systems such as the Colorado, show substantial declines or even extinctions of indigenous species, and their subsequent replacement by exotic species better adapted to the new conditions (Carlson and Muth 1989). Nevertheless, even in those rivers where no losses have occurred, substantial alterations in relative species dominance have been noted. These follow a standardized pattern as conditions in modified rivers with regulated flows are similar.

Within the modified channels there is a tendency to lose obligate migratory species although management is usually directed at their protection through installation of fish pass structures or through stocking. There is a tendency for dominance in fish assemblages to shift from floodplain spawners (phytophilous species) towards main channel spawners (mainly lithophils). It seems too as if many riverine fishes exist in two behavioural morphs, one of which is adapted to the main channel, the other to the floodplain. In some rivers, such as the Niger, this differentiation occurs at the species level (Dansoko et al. 1976; Welcomme 1985). Usually, however, distinction is made intraspecifically. For example, populations of the anadromous *Hilsa ilisha* in Indian rivers have both migratory and territorial components (Pillay and Rosa 1963). Stott (1967) observed similar phases in populations of the relatively static *Rutilus rutilus* and *Gobio gobio* in Europe, observations which have since been extended to *Stizostedion lucioperca* (Fickling and Lee 1985). Similar observations were made on the Volga by Pavlov and Vilenkin (1989) who state that the proportion of the population which is mobile differs according to species. The status of these behavioural morphs is far from clear but it appears that even though an individual species may not be lost to the fish assemblage, some forms of that species may do so.

In impounded reaches and especially in reservoirs, similar population shifts have occurred throughout the world. These involve a rise to dominance of littoral, demersal species, usually comprising the same mainstream spawners that are common in the modified river channel, and the emergence of pelagic planktonophage species which normally constitute a very minor part of a fish assemblage in unmodified streams. Thus in the Volga River, populations of immigrant species *Osmerus eperlanus* and *Clupeonella delicatula*, have occupied the pelagic zones of the reservoirs. *Dorosoma* or *Osmerus* spp. have occupied the pelagic zones of reservoirs on the Tennessee (Voigtlander and Poppe 1989), Missouri (Hesse et al. 1989), and Colorado (Carlson and Muth 1989) rivers. In Africa, it is recognized that pelagic fisheries based mainly on freshwater clupeids constitute a major fisheries resource in most reservoirs (Kapetsky and Petr 1984).

Biotic Stresses

The biotic category of stresses such as nutrient enrichment or fishing, act directly on fish assemblages. They tend to be diffuse, with an effect that is continuous and proportional to intensity. The evolution of multi-species fish assemblages under exploitation in some Canadian lakes were described by Regier and Loftus (1972) who attributed the changes that occurred to the "fishing-up process". Regier and Henderson (1973) further conceptualized these changes and a generalized model was elaborated to describe them. Other indications of the way in which the components of complex fish assemblages react under fishing and environmental pressures could be assembled from numerous sources, for example Lake Tanganyika (Coulter 1970), the Caspian Sea (Carre 1978), Lake Malawi (Turner 1981), the Nile (Borhan 1981), Lake Victoria (Witte and Goudswaard 1984), the Oueme River (Welcomme 1985), and a series of Polish lakes (Bninska 1985).

The model which emerges from these various bits of evidence indicates that catch from multi-species fisheries rises sharply to a maximum as pressure is first applied to the fishery but thereafter can remain at a moderately constant level over a considerable range of effort. This system conservatism conceals biological adjustments made within the structure of the fish assemblage. The model proposes that there is a succession in predominance which arises as each species passes in turn through a typical fish production curve of catch against effort. In general, large fishes tend to be more vulnerable to external pressures than small ones. Thus as fishing effort increases, the large specimens and species are progressively eliminated from the fishery. As a result, mean length of the fish caught drops, species diversity rises initially but then falls and the assemblage as a whole is forced from dominance by '*K*' selected species towards '*r*' selected species. These changes imply an accelerated rate of biological production and a drop in standing stocks with corresponding changes in the P/B ratio. Losses of larger fishes are generally ascribed to gear selective fisheries where progressive lowering of mesh sizes may accelerate the trend. However, the same effects have been observed in fisheries, such as those of the Oueme or the Niger rivers where a full range of gears covers all species and size-classes simultaneously, which would argue that the fishing-up process is not just an artifact produced by a particular pattern of gear use, but is applicable to multi-species fisheries in general. As the fishing-up process proceeds, the abundance of fishes as reflected by the catch, tends to destabilize because the assemblage becomes more sensitive to year-to-year fluctuations arising from annual differences in flood strength.

There is evidence that similar successions of events are produced by other pressures such as nutrient enrichment. Furthermore, other organisms appear to behave in much the same manner as fishes. For example, Payne (1986) notes several examples of parallel changes among grazed phytoplankton communities. Discussions during LARS also indicated that a similar pattern of change has been observed at the stock level within individual species of salmonids from Western American rivers. Further support for this concept was forthcoming during LARS where individual river systems showed at least some of these trends. The fish assemblage of the Vistula River had progressively lost its larger and more active species in the face of pollution (Backiel and Penczak 1989). The pattern of fishing had changed with a diminution in the commercial fishery and a considerable increase in the recreational fishery, although catches of non-migratory species had remained more or less constant since about 1964. The Danube fishery too, has maintained a relatively constant level of catch despite changes in the environment and in the fishery itself. There, larger migratory species have also disappeared (Bacalbaşa-Dobrovici 1989). In the Magdalena River there has also been a major decline in the fishery for larger migratory fishes although catches from the more diverse lagoon fishery had changed relatively little (Valderrama and Zarate 1989). A similar loss of large species has been noted from areas close to the main fishing centres of the Amazon River (Bayley and Petrere 1989). Populations of the large major carps and the migratory *Hilsa* of the Ganges have declined much in recent years in response to heavy fishing and inordinately high levels of pollution and enrichment. Nevertheless, the increase in abundance of the small carps and air-breathing species has been such as to maintain the catch in the face of sustained high levels of effort (Natarajan 1989). Comparison between two reaches of the Orinoco (Novoa 1989) illustrate how differences in fishing intensity can affect the composition of the fish assemblage. The lightly fished western portions of the river show little modification whereas the lower, eastern reaches show the decline of large species and reduction in mean length or catch associated with heavy fishing. Even so, landings have remained relatively constant or have even risen with a two-fold increase in effort. From the foregoing, it may be concluded that this general model of the dynamics of fish assemblages in rivers under biotic stresses is a useful conceptual tool.

Postscript

Our present capability to evaluate biotic assemblages and ecosystem metabolic interactions of large rivers is severely limited by our inability to interpret the complex spatial and temporal heterogeneity along the length of the river. The challenge for future research will be to determine how ecologically important processes at the local level can be aggregated to explain system-wide responses within the river basin. This will need close and continued collaboration among the scientists of a number of different disciplines such as ecology, river limnology, fisheries, biogeochemistry, climatology, geology, engineering, and geomorphology. How the different approaches may be integrated among the various disciplines presents a formidable challenge for the future.

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References

Amoros, C., A. L. Roux, J. L. Reygrobellet, J. P. Bravard, and G. Patou. 1986. A method for applied ecological studies of fluvial hydrosystems. Regulated Rivers 1(1): 17–36.

Annibal, S. R. 1983. Avaliacao bio-ecologico e pesqueira das "pescadas" (*Plagioscion squamosissimus* Heckel 1840 e *Plagioscion montei* Soares 1978) no "sistema Lago do Rei" — Ilha do Careiro — AM — Brasil. INPA, Manaus, M.S.C. dissertation., Pag. Var.

Bacalbaša-Dobrovici, N. 1989. The Danube and its fishery, p. 455–468. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Backiel, T., and T. Penczak. 1989. The fish and fisheries in the Vistula River and its tributary the Pilica River, p. 488-503. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Bayley, P. B., and M. Petrere Jr. 1989. Amazon fisheries: assessment methods, current status and management options, p. 385-398. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Bodaly, R. A., J. D. Reist, B. M. Rosenberg, P. J. McCart, and R. E. Hecky. 1989. Arctic rivers: Fish and fisheries of the Mackenzie and Churchill Rivers, p. 128–144. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Borhan, M. A. 1981. River Nile fish and fisheries 1980. Institute of Oceanography and Fisheries, Inland waters and fish culture branch, Progress rep. 5. Pag. var.

Bninska, M. 1985. The effect of recreational uses upon aquatic ecosystems and fish resources, p. 223–235. *In* J. S. Alabaster [ed.] Proc. EIFAC Symp., FAO/Butterworth, London.

Bravard, J. P., C. Amoros, and G. Palitou. 1986. Impact of civil engineering works on the succession of communities in a fluvial system. A methodological and predictive approach to a section of the Upper Rhone River, France. Oikos 47: 92–111.

Brousseau, C. S., and G. A. Goodchild. 1989. Fisheries and yields in the Moose River Basin, Ontario, p. 145-158. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Carlson, C. A., and R. T. Muth. 1989. The Colorado River: Lifeline of the American Southwest, p. 220–239. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Carre, F. 1978. La perche en Mer Caspienne. Ann. Geograph. 479: 1–39.

Coulter, G. W. 1970. Population changes within a group of fish species in L. Tanganyika following their exploitation. J. Fish. Biol. 2: 329–353.

Dansoko, F. D., H. Breman, and J. Daget. 1976. Influence de la secheresse sur les populations d'*Hydrocynus* dans le Delta Centrale du Niger. Cah. ORSTOM Hydrobiol. 10(2): 71–76.

Davies, B. R., and K. F. Walker. 1986. The ecology of river systems. Monographiae Biologicae (30), Junk, Dordrecht. 793 p.

Ebel, W. J., C. D. Becker, J. W. Mullan, and H. L. Raymond. 1989. The Columbia River — towards a holistic understanding, p. 205-219. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Fickling, N. J., and R. L. G. Lee. 1985. A study of the movement of the zander, *Lucioperca lucioperca* L., population of two lowland fisheries. Aquacult. Fish. Manage. 16: 377–393.

Fremling C. R., J. L. Rasmussen, R. E. Sparks, S. P. Cobb, C. F. Bryan, and T. O. Claflin. 1989. Mississippi River fisheries: A case history, p. 309-351. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environ. Manage. 10(2): 199–214.

Gibbs, R. J. 1970. Mechanisms controlling world water chemistry. Science 170: 1088–1090.

Hesse, L. W., J. C. Schmulbach, J. M. Carr, K. D. Keenlyne, D. G. Unkenholz, J. W. Robinson, and G. E. Mestl. 1989. Missouri River fishery resources in relation to past, present and future stresses, p. 352-371. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Holčík, J., and I. Bastl. 1977. Predicting fish yield in the Czechoslovakian section of the Danube River based on the hydrological regime. Int. Rev. Gesamten Hydrobiol. 62(4): 523–532.

Junk, W. J., P. B. Bayley, and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems, p. 110–127. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Kapetsky, J. M., and T. Petr. 1984. Status of African reservoir fisheries. CIFA Tech. Pap. 10: 326 p.

Kellerhals, R., and M. Church. 1989. The morphology of large rivers: characterization and management, p. 31–48, *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Krykhtin, K. L. 1975. Causes of periodic fluctuations in the abundance of the non-anadromous fishes of the Amur River. J. Ichthyol. 15(5): 826–829.

Lelek, A. 1989. The Rhine River and some of its tributaries under human impact in the last two centuries, p. 469–487. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Liao, G., K. Lu, and X. Xiao. 1989. Fisheries resources of the Pearl River and their exploitation, p. 561–568. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Limburg, K. E., S. A. Levin, and R. E. Brandt. 1989. Perspectives on management of the Hudson River ecosystem, p. 265-291. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Lindeman, R. 1942. The tropho-dynamic aspect of ecology. Ecology 23: 399–418.

Malvestuto, S. P. and E. K. Meredith. 1989. Assessment of the River Niger fishery in Niger (1983–1985) with implications for management, p. 533–544. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Mann, R. H. K. 1989. The management problems and fisheries of three major British rivers: the Thames, Trent and Wye, p. 444–454. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Maybeck, M. 1979. Concentrations des eaux fluviales en elements majeurs et apports en solution aux oceans. Rev. Geol. Dyn. et de Geog. Phys. 21(3): 215–246.

Minshall, G. W., K. W. Cummins, R. C. Peterson, C. E. Cushing, D. A. Bruns, J. R. Sedell, and R. L. Vannote. 1985. Developments in stream ecosystem theory. Can. J. Fish. Aquat. Sci. 42(5): 1045–1055.

Mollard, J. D. 1973. Air photo interpretations of fluvial features. National Research Council of Canada, Associated Committee on Geodesy and Geophysics, Subcommittee on Hydrology, 7th Canadian Symposium Proceedings: 341–380.

Naiman, R. J., J. M. Melillo, M. A. Lock, T. E. Ford, and S. R. Reice. 1988. Longitudinal patterns of ecosystem processes and community structure in a sub-arctic river continuum. Ecological Monographs, Junk, The Hague. (In press).

Natarajan, A. V. 1989. Environmental impact of Ganga Basin development on gene-pool and fisheries of the Ganga River System, p. 545-560. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Northcote, T. G., and P. A. Larkin. 1989. The Fraser River: A major salmonine production system, p. 172-204. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Novoa, D. 1989. The multi-species fisheries of the Orinoco River: development, present status and management strategies, p. 422-428. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Oglesby, R. T., C. A. Carlson, and J. A. McCann. 1972. River ecology and man. Academic Press, New York, NY.

Pavlov, D. S., and B. Y. Vilenkin. 1989. Present state of the environment, biota and fisheries of the Volga River, p. 504–514. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Payne, A. J. 1986. The ecology of tropical lakes and rivers. John Wiley and Sons, New York, NY. 301 p.

Pillay, S. R., and H. Rosa Jr. 1963. Synopsis of biological data on hilsa, *Hilsa ilisha* (Hamilton, 1822). FAO Fish. Biol. Synop. 25: pag. var.

Quirós, R., and C. Baigun. 1985. The fisheries and limnology of the lower Plata Basin. Trans. Am. Fish. Soc. 114: 377-387.

Quirós, R., and S. Cuch. 1989. The fishery of the lower Plata River basin: fish harvest and limnology, p. 429–443. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Randall, R. G., M. F. O'Connell and E. M. P. Chadwick. 1989. Fish production in two large Atlantic coast rivers: Miramichi and Exploits, p. 292–308. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Rapport, D. J., H. A. Regier, and T. C. Hutchinson. 1985. Ecosystem behaviour under stress. Nat. 125(5): 617–640.

Regier, H. A., and H. F. Henderson. 1973. Towards a broad ecological model of fish communities and fisheries. Trans. Am. Fish. Soc. 102(1): 56–72.

Regier, H. A., and K. H. Loftus. 1972. Effects of fisheries exploitation on salmonid communities in oligotrophic lakes. J. Fish. Res. Board Can. 29: 959–968.

Roux, A. L., C. Amoros, M. Richardot-Coulet, J-L. Reygrobellet, G. Pautou, and J. P. Bravard. 1982. Cartographie polythematique apliquée a la gestion écologique des eaux. Paris CNRS: 104 p.

Roy, D. 1989. Physical and biological factors affecting the distribution and abundance of fishes in rivers flowing into James Bay and Hudson Bay. p. 159-171. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Ryder, R. A., S. R. Kerr, K. H. Loftus, and H. A. Regier. 1974. The morphoedaphic index, a fish yield estimator — review and evaluation. J. Fish. Res. Board Can. 31(5): 663–688.

Ryder, R. A., and J. Pesendorfer. 1989. Large rivers are more than flowing lakes — a comparative review. p. 65–85. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Schlesinger, D., and H. A. Regier. 1982. Climatic and morphoedaphic indices of fish yields from natural lakes. Trans. Am. Fish. Soc. 111: 141–150.

Stott, B. 1967. The movements and population densities of roach (*Rutilus rutilus* (L.)) and gudgeon (*Gobio gobio* (L.)) in the river Mole. J. Anim. Ecol. 36: 407–423.

Turner, J. L. 1981. Changes in multispecies fisheries when many species are caught at the same time. *In* J. M. Kapetsky [ed.] Seminar on river basin management and development. CIFA Tech. Pap. 8: 30 p.

Valderrama, M., and M. Zarate. 1989. Some ecological aspects and present state of the fishery of the Magdalena River basin, Colombia, South America, p. 409–421. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. Can. J. Fish. Aquat. Sci. 37(1): 130–137.

Vidy, G. 1983. Pêche traditionnelle en bordure du Grand Yaeres nord-camerounias: Le Logomatia. Rev. Hydrobiol. Trop. 16(4): 353–372.

Voigtlander, C. W., and W. L. Poppe. 1989. The Tennessee River, p. 372–384. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Ward, J. V., and J. A. Stanford. 1989. Riverine ecosystems: The influence of man on catchment dynamics and fish ecology, p. 56–64. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Welcomme, R. L. 1976. Some general and theoretical considerations on the fish yield of African rivers. J. Fish. Biol. 8: 351–364.

1979. Fisheries ecology of floodplain rivers. Longman, London. 317 p.

1985. River fisheries. FAO Fish. Tech. Pap., (262): 330 p.

1989. Review of the present state of knowledge of fish stocks and fisheries of African rivers, p. 515-532. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Whitton, R. B. [ed.]. 1975. River ecology. London, Blackwell, 725 p.

Witte, F., and P. C. Goudswaard. 1984. Prospects of the haplochromine fishery in southern Lake Victoria. HEST Report No. 33. Leiden University, The Netherlands. Pag. Var.

Management of Fish Populations in Large Rivers: A Review of Tools and Approaches

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Abstract

PETTS, G. E., J. G. IMHOF, B. A. MANNY, J. F. B. MAHER, AND S. B. WEISBERG. 1989. Management of fish populations in large rivers: a review of tools and approaches, p. 578–588. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

In common with most branches of science, the management of riverine fish populations is characterised by reductionist and isolationist philosophies. Traditional fish management focusses on stocking and controls on fishing. This paper presents a concensus of scientists involved in the LARS workshop on the management of fish populations in large rivers. A move towards a more holistic philosophy is advocated, with fish management forming an integral part of sustainable river development. Based upon a questionnaire survey of LARS members, with wide-ranging expertise and experience from all parts of the world, lists of management tools currently in use are presented. Four categories of tools are described: flow, water-quality, habitat, and biological. The potential applications of tools for fish management in large rivers is discussed and research needs are identified. The lack of scientific evaluations of the different tools remains the major constraint to their wider application.

Résumé

PETTS, G. E., J. G. IMHOF, B. A. MANNY, J. F. B. MAHER, AND S. B. WEISBERG. 1989. Management of fish populations in large rivers: a review of tools and approaches, p. 578–588. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Comme pour la majorité des domaines scientifiques, la gestion des populations de poisson des grands cours d'eau se caractérise par l'application des concepts du réductionnisme et de l'isolationnisme. La gestion classique met l'accent sur l'ensemencement et la réglementation des pêches. Le présent document résume les vues partagées par les scientifiques ayant participé à l'atelier de travail du symposium LARS sur la gestion des populations de poisson des grands cours d'eau. On propose une approche plus globale où la gestion du poisson fait intégralement partie de la mise en valeur soutenue du cours d'eau. Des listes des outils de gestion actuellement utilisés sont présentées. Celles-ci ont été établies à partir d'une enquête par questionnaires auprès des participants au symposium qui provenaient de diverses parties du monde et dont les connaissances et expériences couvraient une très large gamme. On décrit quatre catégories d'outils ayant trait à l'écoulement, à la qualité de l'eau, à l'habitat et aux paramètres biologiques. On traite des applications possibles de ces outils à la gestion du poisson dans les grands cours d'eau et détermine les besoins de la recherche. L'absence d'évaluations scientifiques de ces diverses approches continue d'être la principale contrainte à l'élargissement de leur application.

Introduction

During the last 10 years there has developed a greater awareness of the problems of water and land resource development for riverine ecosystems (Davies and Walker 1986; Petts 1984; Ward and Stanford 1979; Welcomme 1979; Whitton 1984). With this has come a recognition of the urgency which is needed in managing (protecting, maintaining, enhancing, and restoring) fish populations and their environments within large rivers. Conservation issues have become important for some societies, but the consequences of development on fish health and population structure, including reduced catches and disappearance of native species, have largely been ignored. This is due to several reasons: first, the lack of societal concern for river ecology (cf. terrestrial ecosystems) which is related to the need for water development to sustain economic growth; secondly, the inability of science precisely to predict the ecological impacts of water development; and thirdly, the failure of scientists to communicate ecological needs effectively to decision makers and the public. Science is not — and should not be — concerned solely with management problems, but management needs and opportunities should be considered, and scientists must be prepared to communicate their findings convincingly to all those concerned with the decision-making process.

One objective of LARS was to provide a state-of-the-art review of the management of large-river fisheries. The aim of this paper is to review the range of tools and approaches currently used to manage fish populations in large rivers and to identify scientific and management needs for the attainment of sustainable large river development. The paper is a summary of the discussions of a Working Group convened at LARS and of subsequent contributions from subgroups and individuals. Lists of tools and approaches currently in use and a qualitative assessment of their popularity was obtained from a questionnaire survey of all LARS participants. The popularity data must be treated with caution, however. In most cases, 'success' was not quantified and there have been few critical appraisals of the effects of different actions on fish populations, especially with regard to large rivers. Material on applications of tools has been synthesized from all papers presented at LARS; only additional important works are specifically referred to herein.

Impacts on Fish Populations

It is now clear that river management should address problems at a scale larger than that of a short reach of main channel. Large rivers must be viewed as fluvial hydro-systems (Amoros et al. 1987) each consisting of a longitudinal gradient; a transversal dimension — the alluvial plain including all the aquatic, semi-aquatic and terrestrial biotopes and biocoenoses that are interconnected permanently or intermittently with the lotic environment of the main channel; and the vertical dimension of the alluvial subterranean waters and their biological populations. Within this fluvial hydro-system context, fish populations relate to the quantity, quality and stability of the environment. In African Savanna rivers, for example, the annual inundation of the floodplain is vital for sustaining the fish community (Welcomme 1985). The floodplain and the network of connected and isolated ponds (abandoned channels) act as spawning and nursery areas, and provide refuges, for lotic species.

It is widely acknowledged that channelization and flow regulation can be detrimental to lotic ecosystems. For anadromous fish species, dams and weirs isolate headwater spawning and rearing grounds, so that species of Acipenseridae and Salmonidae, for example, have been virtually eliminated from many European rivers. However, such barriers are rarely the only cause of species disappearance from rivers; the creation of lentic reaches, habitat changes within the lotic environments, the altered flow regime, and water-quality changes, are usually involved.

River regulation practices eliminate the hydrological and geomorphological dynamism of the natural hydro-system and isolate the main river from the alluvial plain, markedly changing fish populations. Welcomme (1985) reports that 6000 tons of fish have been lost from the Niger River below the Kainji Dam, and the Pa Mong dam on the Mekong River is expected to eliminate flooding for some 700 km downstream, causing a loss of catch of about 2150 tons. In some cases, with careful management (Bernacsek 1984) fish production within the reservoir may replace that lost from the river downstream. However, the downstream losses often surpass the potential of the reservoir itself, and considerable modifications in community structure are involved, as many species are unable to adapt to a lentic environment.

Management requires the diagnosis of the causes of changes in fish communities. Burt and Mundie (1986), in a review of 81 case histories of regulated rivers mainly in the Pacific North West of North America (Table 1), clearly illustrate the need in fish management for the maintenance of hydrological conditions (eg. for salmonids in terms of passage, spawning, incubation and juvenile rearing). However, their review emphasises the difficulties in determining cause and effect relationships. Commonly, biological populations are impacted by the cumulative effect of several, often interdependent and individually low magnitude, hydrological, water-quality, and geomorphological changes.

It is apparent that ecological changes often take place slowly. Ten years or more may be needed before changes can be defined as significant in statistical terms and the complete readjustment of a fluvial hydro-system can require more than 100 years in some cases (Petts 1988). Moreover, absolute causality is often difficult to establish: first, because many rivers have experienced a succession of

TABLE 1. Causes of changes in salmonid populations in regulated rivers (After Burt and Mundie 1986). Percentages relate to proportion of case studies identifying cause as significant.

Effect	Cause	%
Negative		
• Decreased populations		59
	• Hydrological change	35
	• Block migrations	35
	• Sedimentation of habitat	29
	• Thermal changes	17
	• Pollution	6
	• Gravel erosion	4
	• Gas supersaturation	2
Positive		
• Increased populations or no change		18
	• Increased mean annual flows	
	• Increased flows during months in which discharge apparently limited salmonid populations prior to regulation	

impacts during the past 200 years; secondly, because ecological responses involve complex biological and physical changes and interactions; and thirdly, because of the lack of knowledge about the ecological dynamics of large rivers. The first two of these are well illustrated by Petts et al. (1989) for large alluvial rivers in western Europe. The sequence of impacts and the change in attitude of society to river fish populations is illustrated in Fig. 1. Such historical analyses are fundamental for advancing both scientific knowledge and management practice particularly by demonstrating the sensitivity of species and communities to different impacts.

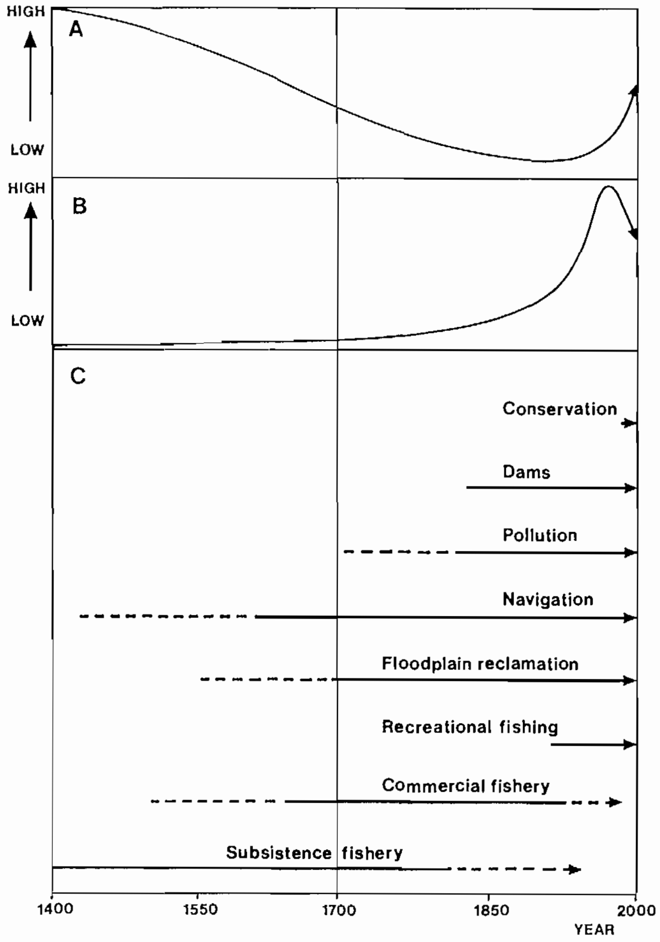

FIG. 1. The historical development of European rivers showing the relative value of fish to society (A), the intensity of impacts of development on fish (B), and the sequence of developments that have affected fish populations (C) — the solid arrows indicate the period of major impact, which may be positive or negative (based upon Petts 1987).

Approaches to Fish Management

Traditionally, the management of riverine fish populations has been directed to achieving either maximum sustainable yields of one or a small group of species, or maximum economic returns: two objectives that are rarely (and then probably coincidentally) compatible. Within these approaches, a riverine fish community may be maintained, for example, by stocking and selective fishing or by fishing controls, or replaced, for example, by aquaculture or by a reservoir fishery. The reductionist philosophy focusses on fish, usually one 'target' species (often to the exclusion of others) within an environment and is responsive to a real, or perceived, need of society. This approach is advocated (possibly inadvertantly) by IBP Handbook No.3 (1978). Fish management tools will remain an important component of any river management plan. However, in regulated rivers it is often impossible to counteract the dramatic changes in fish communities by using these tools alone (Backiel (1985).

An alternative approach is to adopt an holistic philosophy by viewing the fish communities of large rivers within the context of the fluvial hydro-system recognising its functional relationships within the whole catchment ecosystem. The integrated management of hydrology, geomorphology and biology has the objective of optimizing the resource potential of large rivers within a long-term perspective. Such an approach to ecologically sound river development has been discussed by Gore and Petts (1989). The approach utilises a management framework that focusses on the cause(s) of change in fish populations. For sustainable conservation of biological communities, emphasis must be placed on managing first-order impacts on flow, water quality, and sediment transport and their second-order consequences for channel structure (Petts 1984, 1988). The framework has three levels:

1) The first level uses secondary regulation — structural measures and special operational rules for the major project elements — to mitigate ecological impacts. At this level the aim is to sustain the natural process dynamics of the fluvial hydro-system to maintain habitat diversity or to recreate this diversity artificially.

2) The second management level seeks to maintain biological populations directly (eg. by stocking) or by controlling the activities of Man (in this case fishing).

3) At the third level of management, two options are available. The first is to preserve the river in an undeveloped state. The second option is to accept the ecological losses associated with development and to compensate for these losses by preserving the affected biological populations in other rivers, or in artificial water-bodies.

In assessing the impacts of a development and planning their mitigation, or in planning river restoration works, emphasis should be placed on maintaining or enhancing the natural range of habitats in space and their characteristic dynamics through level one management options. Flow and water-quality operate at a large scale and, ideally, any problems of these variables should be resolved before site specific habitat management tools can be effective. Second level management, incorporating most of the actions of traditional fish management, in the first instance, should be considered as complementing level one proposals. The conflicting third level options should be considered only after an imaginative assessment of the full range of options contained within the two higher levels, and only if the first two management levels are expected to fail in their attempts to facilitate conservation and development simultaneously.

Tools for Fish Management

From the survey of LARS members, it is apparent that a range of tools are available to achieve the first and second levels of management. These tools can be classified as: (1)

flow modifications; (2) water quality management, (3) habitat management, and (4) direct controls on fish and fishing. The first three groups deal with fish environment and relate to the first management level. They combine to influence fish habitat and are distinguished for technical rather than ecological reasons. Group 4 relates to the second management level. The tools may be applied before, during or after development to protect or enhance fish yields and stock diversity. In the developed world, for example in Europe where major river channelisation schemes were started in the 18th Century, the focus for management is river restoration, whereas in the Third World opportunities exist for preemptive fish management to influence the planning of catchment developments and water projects. Lists of tools are given in Tables 2, 3, 4, and 5. Alternatives in river regulation are discussed further by Gore and Petts (1989) and a review of river regulation in the United Kingdom provides additional information (Petts and Wood 1988).

Flow Manipulation

The generation of artificial flow conditions to optimise the range of abiotic and biotic parameters that affect fish population dynamics can serve to preserve, rehabilitate, or enhance populations of target species and, potentially, whole communities. Opportunities for fish management involve restructuring the flow regime, with regard to both seasonal and short-term variability, which may or may not require changes to total annual discharge. However, to date, flow manipulation, although relatively common (Table 2), has only rarely been undertaken specifically for fish management and most beneficial effects on fish populations have been coincidental. These benefits have arisen where flow regulation below flood-control or water-supply dams has maintained a minimum flow or, for cold-water fisheries, prevented excessive temperatures during drought (eg. see Petts and Wood 1988).

Where they have been applied, flow regime modifications for fisheries have been intended to mitigate the effects of an existing regulation scheme not the least important of which are those below hydro-electric power and irrigation supply dams (Petts 1984). In the case of the former, daily flow fluctuations, and in the latter a reversal of the natural seasonal flow regime, can be detrimental to fish populations. Clearly, it is important that fishery needs are discussed during the formulation of dam release schedules and in the United States the negotiation of a favourable schedule is part of the licensing procedure for all non-federal hydroelectric power dams (eg. Bowman and Weisberg 1985). Alternatively, whenever short-term flow fluctuations cause flushing and/or dewatering problems below a power-peaking dam, downstream re-regulation weirs have been used to reduce the flow variability (Cushman 1985). These may also be used to generate additional hydro-electricity to offset construction costs.

One important tool is the designation of a minimum flow — and its seasonal variability — necessary to maintain or enhance fish populations. The restriction of water withdrawals appears to be a relatively obvious management tool yet in some river systems, such as the Colorado, demands for water are so great that minimum flows cannot be established (Anderson 1982). Water withdrawals may be compensated by augmenting the annual discharge. Interbasin

TABLE 2. Flow modifications — results from a questionnaire survey of LARS participants. Tools are listed in rank order according to popularity as indicated by the percentage of rivers on which the tool was used. The percentage of rivers where a tool was perceived as a failure is also indicated.

Tool	% of Rivers	% Failure
1. Using run of the river dams and reservoirs:		
• Maintain minimum flow	38	—
• Seasonal water release schedules	24	10
• Maintain maximum daily flow fluctuations	19	—
• Flushing flows for channel maintenance	12	20
2. Flow augmentation by:		
• Inter-basin transfers	10	—
• Aquifer pumping	7	—
• Off-line pump-storage reservoirs	10	—
* The last two tools have been used only on small rivers		
3. Other:		
• Reservoir level regulation	21	11
• Re-regulation dams/weirs	19	—
• Sustain freshwater flow to estuary	7	—
• Draw-down water levels to inhibit spawning of undesirable fish	7	33

TABLE 3. Tools for water-quality management — results from a questionnaire survey of LARS participants. Tools are listed in rank order according to popularity as indicated by the percentage of rivers on which a tool used. The percentage of rivers where a tool was perceived as a failure is also indicated.

Tools	% of rivers	% Failure
1. Flow control:		
• Controlled dilution flows	17	14
• Depth-selective reservoir releases	5	—
2. Gas regulation:		
• Hypolimnetic aeration within impoundments	5	—
• Install re-aeration weirs	5	—
• O_2 injection at turbines or in river	2	—
3. Turbidity controls:		
• Sediment traps/settling ponds	14	—
• Dredge polluted sediments	14	—
• Structures to reduce fetch	5	—
4. "Solute" controls:		
• Use wetlands for water purification	10	—
• Add nutrients to stimulate productivity	5	—
• Liming to increase pH	2	—
5. Watershed controls:		
• Point-source pollution controls	57	13
• Land-use regulations	29	8

TABLE 4. Tools for habitat management — results from a questionnaire survey of LARS participants. Tools are listed in rank order according to popularity as indicated by the percentage of rivers on which a tool is used. The percentage of rivers where a tool was perceived as a failure is also indicated.

Tools	% of Rivers	% Failure
A. Management of habitat for fish:		
• Rip-rap the banks	36	7
• Add substrate (eg. spawning gravel)	26	9
• Structures to improve habitat	24	16
— wing dikes - groynes	21	22
— instream bed-control structures	17	—
— marginal bank-parallel dikes	12	40
— snags	7	—
• Excavate side channels	21	11
• Plant riparian vegetation	17	6
• Create new spawning channels	17	14
• Limit size and spread of vessels to prevent bank erosion	17	43
• Construct islands	12	—
• Introduce macrophytes	9	—
• Dredge pools	5	—
• Introduce invertebrates	5	—
B. Management of developments that affect fish:		
1) Dam by-passes and intake screens:		
• Ladders	33	29
• Screening to reduce entrainment at intakes	26	27
• Screening to prevent impingement	21	22
• Locks	14	—
• Devices to guide fish into passes	14	17
• Fish lifts and transport	12	—
• Reservoir spill to pass smolts	5	—
• Juvenile by-pass facilities	5	—
2) Floodplain management		
• Re-establish access to backwaters	29	25
• Excavate floodplain ponds	14	17

transfers are increasingly being used for water redistribution (Golubev and Biswas 1985; Newbury et al 1984) although opportunities for fish management are yet to be exploited. Similarly, Wright and Berrie (1987) have demonstrated the potential utility of aquifer pumping to maintain minimum flows during periods of extreme drought. However, flow augmentation schemes can cause adverse impacts both in the receiving stream and as a result of the loss of water from the source area. In the Churchill River diversion project, increased flow led to an increase in shoreline erosion, turbidity, and contaminant concentrations, and a general negative impact on fisheries (Bodaly et al. 1984a, b).

Criteria for flow requirements

Notwithstanding the problems of water quality described below, the implementation of flow modification techniques presupposes that appropriate minimum flows, maximum flows, and the degree of flow fluctuation to protect or enhance fish populations can be quantified. In practice, tools to do so are only now being developed. For many species, little is known about how flow affects abundance, growth, etc. and flow requirements for fish are often based on indirect methods, such as the Tenant Method (see Wesche and Rechard 1980), which calculate minimum flow as a flow duration or frequency statistic. However, these approaches assume that retaining some existing hydrological condition will be beneficial to the fish; only rarely has this been demonstrated (Annear and Conder 1984).

TABLE 5. Controls on fish and fishing — results a questionnaire survey of LARS participants. Tools are listed in rank order according to popularity as indicated by the percentage of rivers on which a tool is used. The percent of failures as perceived by respondents is also indicated.

Tools	% of Rivers	% Failures
1. Controls on activities of people:		
• Closed seasons	69	7
• Size limits	67	14
• Catch quotas	62	8
• Closed areas	57	7
• Gear restrictions	52	18
• Restrict fish harvest	38	6
• Baitfish control	31	22
• Ban collection of larval fish	17	—
• Ban fish poisons	3	—
2. Controls on numbers of people:		
• Licence control	33	7
• Limit access to water	19	12
3. Controls on fish:		
• Stocking of exotics	45	6
• Put and take fishery	40	25
• Protect rare fish	36	20
• Remove undesirable fish	31	15
• Reduce over-abundant fish	14	15
• Floodplain aquaculture	14	15
• Stocking of natives	5	50

Few approaches for setting flow requirements are based on the biology of fish. Empirical evidence for benefits that may be derived from a limited number of alternative flows, which may or may not include the optimal flows, can be obtained in two ways. First, data can be derived from a comparison of the survival of target species among years in which different flow conditions are naturally prevailing. Secondly, experimental manipulation can be used to examine the response of the fish community to a range of flow conditions for a limited period of time. The latter requires that other water users agree (or can be coerced!) to cooperate with such experiments.

Solutions to technical problems of assessing instreamflows were discussed at the Boise Symposium (Orsborn and Allman 1976). Subsequently, a diversity of methodologies has been developed. The most widely reported of these is the instream flow incremental methodology (IFIM). This method combines a mathematical model of physical aspects of the river with a model of fish habitat preference to describe the response of fish habitat to changes in flow conditions. Whilst providing a quantitative assessment of habitat available to a target fish over a wide range of possible flow conditions, the method does not yet present a panacea for resource managers (Mathur et al. 1985; Orth 1987). First, the preferred flow and habitat requirements of most species, especially for large rivers, are unknown. Secondly, the model has been validated in a few cases only.

Even when quantitative models are used, many subjective decisions are still necessary to establish flow requirements. For instance, a target species may need to be identified, because flow conditions that benefit one species may be detrimental to another. Some species may be temperature-limited, others space-limited, and yet others food-limited (Weisberg and Lotrich 1986) and it is not yet clear which of these potentially limiting factors should be maximized in application of the models. Indeed, when complex fish communities are considered, it may be that semi-quantitative approaches, similar to the habitat-quality index (Binns and Eiserman 1979), are most useful in river management. Due consideration should be given to the spatial distribution of species throughout the river network as, for example, management of flow releases for downstream fish may cause reservoir fluctuations that affect the success of upstream fisheries (Morgensen 1984). Gore and Judy (1981) concluded that the management of reservoir releases with due consideration for the flow requirements to maintain fish stocks and habitats should result in effective streamflow management.

Water Quality Control

At some point in the developmental stage of a catchment, pollution can become the single biggest problem facing the fisheries manager. Along regulated rivers point and non-point pollution, involving eutrophication (Decamps 1979) and including accidental spillages of toxic wastes, and salt-water incursion to the lower river (eg. Din 1977), can markedly impact fish populations. There are numerous instances where pollution has either closed fisheries of large rivers by direct contamination, for example, polychlorinated biphenyls [PCBs] in the Hudson River (White et al. 1985) and where point source BOD loads have blocked migration routes of fish, such as along the Delaware River (Chittenden 1971). A number of tools are in use for water-quality control (Table 3) but with few exceptions, the most notable of which is gas regulation, they have been used for fish management only rarely.

Legislation for land-use management at the catchment scale, effluent controls and urban runoff regulation can have considerable benefit for lotic ecosystems, albeit often incidentally. Indeed, the rapid spread of sewerage treatment facilities and then the upgrading of treatment plants to secondary and tertiary treatment have probably done more for the recovery of fish populations in rivers than all other management tools combined. Other technological developments for industrial waste water treatment, for example to control mill effluent, heavy metal loadings, and thermal pollution, similarly, have important positive impacts.

Some countries have specific water-quality standards for dissolved oxygen and temperature with respect to fish. DO standards, for example, have been set to protect fish and aquatic life, giving due consideration to life-cycle requirements and to the thermal regime (see Welch 1980 for a review of this issue). However, standards for toxicants are often undefined or ill-defined and this is problemmatic not least because of our limited understanding of the effects of bio- and geo-magnification. Indeed, highly mobile, long-lasting, synthetic organic chemicals, which create long-life residues, may pose the major challenge for management. To overcome the problems of defining acceptable pollution levels, and to avoid degradation where present conditions exceed minimum levels established in receiving water standards, technology-based regulations are often used.

Impoundments are often the source of downstream water-quality problems, but in some instances they may also provide potential solutions. Below deep reservoirs, hypolimnial discharges low in oxygen may cause problems, as can gas supersaturation by hydro-power dams (Ebel 1969; Pettersen and Mellquist 1984). DO levels can be controlled by improving turbine design or by fitting aeration devices, and re-regulation weirs can be effective reaeration structures. Selective withdrawal from dams with multiple draw-off valves allows mixing of water from epilimnial and hypolimnial sources before discharge to the downstream river. However, the use of controlled releases to maintain water quality within the receiving stream can be problematic. With regard to water temperature, Larson (1984) has shown that reservoir-release strategies are capable of optimising water temperatures only within a distance of about 50–60 km below the Lost Creek Reservoir on the Rogue River, USA.

The maintenance of a minimum flow is assumed to be a major benefit of river regulation because, if it is aerated, the flow can provide dilution of some wastes. In practice, the elevation of 'low flow' can reduce both the reaeration of the water, because the oxygen exchange at the surface is distributed over a greater depth, and the residence time between two points of waste injection, so that BOD could be increased below the downstream point source (Gras and Albignat 1985). Thus, the provision of a minimum flow is not *a priori* an appropriate water quality control for regulated rivers receiving urban and industrial effluents, or irrigation return water.

Habitat Management

Fish habitat is here defined as all aquatic environments occupied by fish during all life stages, and includes the critical requirements of habitats for reproduction, migration, growth and survival. The emphasis is on channel and floodplain configurations that determine the hydraulic characteristics of a particular discharge. The general goal is to maintain or create sufficient diversity and quality of habitats to sustain a diverse indigenous fish fauna. A range of tools has been used (Table 4) and these can be grouped into two management pathways, namely: those tools that are used to manage fish habitat directly and those that are used to manage developments and resource uses that affect fish habitat. Once again it is difficult to assess the success of the various tools because field evaluations are the exception and not the rule.

Managing Habitat for Fish

These tools have been used primarily in developed countries where large rivers have been extensively modified by Man. Nevertheless, consideration of the full range of management tools at the planning stage of a project can help to mitigate against detrimental impacts. The management of habitats for fish requires the identification of critical habitats and methods for the protection, maintenance, rehabilitation and enhancement of these areas. Such habitats, particularly spawning grounds and fry habitat, often act as regulators of fish populations but are usually the first to be damaged by physical alterations of rivers and are often the primary areas requiring rehabilitation. Site specific management, to a large extent following closely the work of Swales and O'Hara (1980), is now used quite widely to mitigate the effects of channelisation, and new developments continue to be made (see Gore and Petts 1989).

Clearly, the ideal "tool" is the maintenance of dynamic channel conditions which result in channel and floodplain diversity. Although some 'wild rivers' have been designated for conservation in their natural state, in most cases the preservation of a river system is totally incompatible with development. In these circumstances, tools are required to recreate, as closely as possible, the conditions of the natural river (Sedell and Luchessa 1982). In particular, attention must be given to shelter areas, spawning areas, and food organism requirements. For example, channel bank protection often involves the use of rip-rap and armour stone which, providing a range of stone sizes are used, can realise the twin objective of edge diversity and bank protection. In contrast, concrete mats or interconnecting blocks, although controlling erosion, provide little habitat diversity.

The indented shoreline and floodplains of unaltered rivers appear to be the most important habitat areas of large rivers, not least for "black fish" (Welcomme 1985). The creation and reestablishment of connections from the river channel to the floodplain shows great promise, especially within heavily regulated rivers. Along the Rhine, channels and floodplain lakes isolated by channelization have been reconnected to improve habitat; new ponds have been excavated along the Danube for fish production; and in areas of inundated floodplains along the Missouri and Mississippi dredged sand has been used to create islands to reduce wind fetch, reduce erosion, and enhance habitat.

Instream habitat diversity can be enhanced by wood or concrete structures and gabions (wire baskets filled with rocks) forming check dams, wing deflectors, or mid-channel 'V' deflectors. The main benefit from these structures is the creation of scour holes (shelter areas) and riffle areas for food organisms. For example, along the Missouri and Mississippi rivers modified wing dykes have been used extensively to diversify instream habitats. Evaluation has been somewhat more rigorous than other techniques and good design and implementation information is available (Schnick et al. 1982). The restoration of channel-bed diversity can also be achieved by the addition of graded substrate and the construction of 'artificial riffles'. The latter have enhanced invertebrate production and thus, theoretically, fish production. An alternative approach is to construct new spawning channels, and these have been successful on several large rivers, notably the Fraser and Volga. However, the maximum use of such facilities requires a detailed knowledge of the needs of particular species, and cleaning them may be a substantial and expensive undertaking.

Managing Developments that Affect Fish

Dams and wiers can provide barriers to fish movement, whilst canals can allow the movement of fish between drainage systems — purposefully or inadvertently. Indeed, a number of inter-basin transfers have been stopped because of concerns that introductions of exotic fish species or of parasites could lead to declines in native fishes (Arai and Mudry 1983). Moreover, intakes to thermal power stations can remove significant numbers of fish, fish eggs and larvae, and the passage of fish through hydro-power turbines can cause significant mortalities. A variety of methods are used to reduce fish impingement and entrainment. For example, screens have been used to prevent fish from entering diversions or intakes but screen performance and criteria must be matched to each site and to each species. In any case, intake siting and design are most important.

Fish passage facilities (ladders, locks, lifts, and collection and trucking) have been used with varying success. Experimentation during the 1960's, in particular on the Snake–Columbia system, revealed that the primary problem appears to be the ability of the fish collection system to intercept, or to attract, migrants by providing entrances at proper locations and with suitable hydraulic conditions. The design and efficiency of fishways are dependent on a detailed knowledge of the swimming capabilities and behaviour of migrating fish. For many species this knowledge is unavailable and the effectiveness of any facilities will be uncertain at the planning stage. Moreover, Pelz (1985) has demonstrated that even though fish passes can be installed to mitigate barrier effects, their installation may not be justified unless appropriate hydrological and water quality management is introduced first. Consequently, and because of the costly nature of fish passage facilities, only rarely have they been incorporated into relatively high-level dams (Bishop and Bell 1978).

Controls on Fish and Fishing

Eighteen tools have been used more or less widely but with the exception of banning coollection of larval fish, they are not specific to rivers (Table 5). Controls on the activities of people appear to have been employed with the greatest relative success, especially closed seasons, closed areas and catch quotas. The control of access through licensing remains one of the most important managerial tools, particularly for commercial or recreational fisheries (Welcomme 1985). A form of access control is practised by many traditional fisheries whereby individuals or small groups of fishermen husband clearly defined areas. In many cases, especially in artisanal fisheries, the necessary legislation requires costly, and often logistically problematical, enforcement programs. Indeed, regulations tend to break down under the pressure of unstable socio-economic conditions. It is now clear that in the Third World effective management of riverine fisheries requires greater consideration of the knowledge and institutional structure of local fishing communities (Scudder and Conelly 1985).

Stocking is being used in many large rivers. The general practice of stocking in freshwater, involving both the release of cultivated fish and fish transfer from one water body to another, has received careful examination (EIFAC 1982; 1984) but opinions on the efficacy of the tool still vary. The introduction of exotic species (especially *Salmo* spp.) to capitalize on altered hydrological and thermal regimes has been particularly successful in the tail-waters of some dams.

However, uncritical introductions have been blamed in some cases for the degradation of fish community structure. The stocking of large rivers to maintain or improve their fish stocks is not yet a widespread practice, but in 12 European countries 15 species of fish are being stocked (EIFAC 1982). Stocking with anadromous fish such as sturgeon in eastern Europe and salmonids in the Baltic region has been apparently successful but assessments vary greatly. Nevertheless, the tool seems to have considerable potential both to maintain production in the face of intensive exploitation and to compensate for the adverse effects of human impacts.

Stocking requires the development of aquaculture to produce fish for release into rivers and reservoirs, a technique that can be too expensive for all but the most highly valued species, unless subsidized by other means. The use of artificial fertilisation, incubation and concentrated feed based on studies of fish nutrition has led to the progressive intensification of fish culture systems (eg Muir and Roberts 1982). However, in addition to economic considerations, the requirements of fish cultivation (adaptability to environment, high growth rate, successful reproduction, resistance to disease and ability to support high population densities etc.) means that only a relatively few fish species are used. Consequently, some species have become widely dispersed in a number of regions worldwide (eg. *Cyprinus carpio*, *Salmo gairdneri* and *Tilapia* spp.), a practice almost invariably detrimental to native fish populations.

Application of Tools

River management is a multi-functional activity within which the management of environment in general and of fish communities in particular has a low priority. In most countries, issues relating to fishery development and fish conservation are subordinate to those of water supply, hydro-electric power, flood-control and navigation. However, societal concern for fish populations is related, in general terms, to the standard of living. Less developed societies are dependent upon fish both as a source of protein and as a factor in the rural economy. Conservation issues become important when once a sustainable economic base has been established, as shown for western Europe (eg. Fig. 1). Historically, these two phases have been separated by a period of ecological degradation.

A wide range of tools are available for the management of fish in large rivers, as indicated in Tables 2–5. Some examples of the application of management tools appropriate to common river developments are given in Table 6. Many of the tools are being used for water-supply, water-quality control, and channel maintenance but, at present, few are being used strictly for fish management. Nevertheless, benefits have arisen incidentally. Although, it would be naive to believe that management tools can be used, in most cases, to maintain or restore biological communities *completely*, the prudent application of different tools at both the first and second levels of management has considerable potential for the establishment, maintenance, or even enhancement of some populations.

TABLE 6. Examples of management tools to mitigate impacts of river development.

Typical effects on riverine habitats	Management tools
a) Channelization	
• Isolation of backwaters, floodplain lakes and marshes	• Set back levees to define areas allocated for conservation
• Changed instream physical habitats	• Reconnect isolated lakes and channels or construct new ones • Use rip-rap, wing dikes, or instream structures to enhance habitat diversity • Create artificial riffles or new spawning channels
b) Impoundment	
• Inundation of lotic reaches, block fish migrations, change water quality	• Design project to protect fisheries • Use fish passage facilities • Design intakes with screens to avoid entrainment
c) Flow regulation	
• Loss of hydrological dynamism	• Define minimum ecological flows
• Changes to physico-chemical regimes	• Allocate water to protect ecology
• Loss of life-cycle triggers • Flow confined to single channel • Dewatering of habitats	• Use re-regulation weirs to reduce short-term flow fluctuations and maintain water-quality • Use tools in a) above to maintain instream habitats
d) Catchment development	
• Changed hydro-geo-chemical regimes	• Use integrated basin management
• Pollution	• Undertake EIA's on all proposed developments • Initiate public education programme • Leave buffer zone along river

Clearly, optimization and flexibility are necessary for successful management. Optimization requires the simultaneous application of several tools. The choice of tools should be made only after studies of the state of, and trends in, fish communities; after due consideration of the likely factors responsible for any observed changes; and then of the feasibility of applying the tool or tools at the appropriate scale. Often such data are lacking but this should not inhibit the application of management tools. Monitoring must be a key component of every management plan. Uncertain effects may be dealt with by the "wait-and-see" approach provided that reasonable provisions are made to take corrective action based on the results of appropriate monitoring. Managers should be willing and able to modify or change a tool or combination of tools if it is unsuccessful, not completely effective, or generates unexpected side effects, and in the light of new scientific knowledge.

The biggest impediment to the application of the management tools listed in Tables 2–5 is the uncertainty associated with their success. This uncertainty reflects in part the poor state of knowledge about the flow, water quality and physical habitat requirements of fish throughout their life cycle.

Until these requirements are better understood, the anticipated benefits of primary tools — managing flow and water-quality — can not be defined quantitatively and these tools are likely to remain underutilised in large rivers. Furthermore, the lack of systematic and critical evaluation of the tools for fish management remains a major limitation to their use. The uncertainty also reflects poor communication among scientists, decision makers and the public, a major stumbling block for achieving ecologically sound river development. Fifty-two per cent of the respondents to the questionnaire considered that more extensive and better environmental education is needed to improve public awareness of fish management problems (see Biette et al. 1989).

There are some instances where priorities in river management are changing. A storage reservoir to ensure adequate flow during the summer migration of steelhead and chinook salmon in the Columbia River is presently being considered for construction on the Yakima River, and 5.674 km^3 of storage have been set aside in the Columbia river system for use in fisheries management (NPPC 1982). In the United States, a number of state laws have established the importance of flow for fisheries (Wright and Wright 1985) and a number of court decisions have recently emphasized the importance of fisheries issues in licensing hydroelectric power dams (Bodi 1985). In the United Kingdom, the *1981 Wildlife and Countryside Act* charged the Water Authorities with the duty to "so exercise their functions... as to further the conservation and enhancement of natural beauty and the conservation of fauna and flora". This Act stimulated a change from river development to river management. Progress towards environmentally sound river management has been gaining pace in the UK (Petts and Wood 1988) and elsewhere (Gore and Petts 1989) in response to improved scientific knowledge; wider public awareness of environmental issues; and to the implementation of Environmental Impact Assessments (EIAs).

Comprehensive Management

For many rivers, management is, at best, event-driven and narrowly concerned with specific anthropogenic activities, such that wider issues are often overlooked. Unified river basin management has received much discussion (eg North et al. 1980), and Wengert (1980) concluded that only rarely is integrated river basin development considered to be the answer for the coordination of management planning. Although inhibited by the socio-political environment, long-range comprehensive planning alone can make adequate provision for aquatic ecosystems.

A comprehensive approach to land and water resource planning requires that river (and floodplain) management has three objectives: first, to maximize the water resource potential in terms of water supply and power production; secondly, to plan development in alluvial plains so as to minimize flood hazard and drainage problems; and thirdly, to protect environmental values — recreational, scenic, ecological, and cultural. Conflicts certainly exist, but within the river- or environmental-corridor concept the above three objectives are weighted equally and management of the corridor should seek to both maximize economic development and to satisfy a variety of (apparently) non-economic — but nonetheless real — human needs (Walesh 1973). Indeed, the rationale for maintaining river corridors does not need to include primarily economic arguements. Positive developments have taken place along several rivers, such as the Thames, UK (Gardiner 1988) and even in some urban park environments where waterfront areas including floodplains are being developed to enhance recreational activities (Allen 1984).

Sound environmental management requires that the river is viewed as part of the Catchment Ecosystem. It is important to remember that the dimensions of fish management often involve more than one state, provincial, or national, government. Almost 30 % of the land area of the earth is drained by the twenty largest drainage systems and it is not surprising therefore to find that large rivers cross governmental boundaries. Indeed, 214 large rivers are shared by two or more countries (Biswas 1983). Fish management tools addressing long-term perspectives across several legal jurisdictions can be applied most successfully by establishing a basin-wide river management commission. In the Third World, in particular, problems of river management relate to the difficulty of applying legislation within large river basins. For example, in the Amazon basin, no concepts exist for the long-term development of fishery which could serve as a basis for the development of management strategies (Junk 1984). However, the recently formulated Environmentally Sound Management of Inland Waters Programme of UNEP seeks comprehensive objectives. The first EMINWA plan aims to promote sustainable development of the Zambezi River basin, involving eight nations, and integrating political, social and economic needs with environmental management. The plan includes the establishment of technical and administrative capabilities for conservation and management of fish genetic resources.

Prospect

During the past two decades, the reductionist approach of environmental scientists has contributed to the lack of research on large rivers (Davies and Walker 1986) and the isolationist attitude resulted in a failure to appreciate the full nature of management problems, needs, and opportunities. Only now is the focus of research expanding to encompass the dynamic interactions that characterise the alluvial plains of large rivers (Decamps 1984). With this holistic philosophy, long-term catchment management plans are needed to avoid the detrimental consequences of future developments on fish populations. Such plans should seek to obtain sustainable development, provide for the effective communication of ecological needs to decision makers and the general public, anticipate losses of essential lotic environments and propose mitigation measures. Management is guided by case-histories, and operational strategies evolve in response to impacts. Thus, historical analyses of impacts and the effects of different management practices should be encouraged. Numerous tools are available to mitigate impacts on, and even to enhance, fish populations; but, in their application, optimization and flexibility are key concepts.

For unmodified rivers, not least those in developing countries, costs of maintenance and rehabilitation of degraded fisheries will be much less if managers can minimize negative impacts through the implementation of appropriate tools early in project development. Lessons learned from other countries would suggest that remediation after an impact is enormously more costly than proper mitigative design before the development of large rivers. It must be remembered, however, that reactive and pro-active management requires an appropriate institutional or legal framework. Too often river management — and especially fish management — is inhibited by socio-political constraints. A strong social, political and economic will is required to protect and enhance fish populations at the same time as planning for major economic developments. If this is not present, little interest or capital will be available for ecological protection or rehabilitation. Clearly, better communication between scientists and decision makers is an immediate priority.

For scientists, four immediate problems must be addressed. First, there is a strong need for well structured research to determine the applicability of transferring and translating the knowledge that has been gained on low order streams to large rivers. Secondly, the need to determine the essential habitat requirements of fish is of paramount importance. Knowledge of fish behaviour in relation to river hydraulics, water quality and fluvial geomorphology is lacking or scarce on many large rivers. Thirdly, the reaction of natural aquatic ecosystems to physical perturbations is not well understood; this knowledge is essential to our ability to preserve, maintain and rehabilitate rivers. Fourthly, the effectiveness of different management tools, singly and in combination, must be evaluated for different rivers and for different management problems. Without such information the development of environmentally sound management plans is certainly problematic and, arguably, impossible.

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References

Allen, L. J. [ed.]. 1984. Urban fishing symposium proceedings. Fisheries Management Section, Am. Fish. Soc. Bethesda, MD. 297 p.

Amoros, C., A. L. Roux, J. L. Reygrobellet, J. P. Bravard, and G. Patou. 1987. A method for applied ecological studies of fluvial hydrosystems. Regulated Rivers 1(1): 17–36.

Anderson, R. L. 1982. Conflict between establishment of instream flow and other waste uses on western streams. Water Resourc. Bull. 18: 61–65.

Annear, T. C., and A. L. Conder. 1984. Relative bias of several fisheries instream flow methods. N. Am. J. Fish. Manage. 4: 531–539.

Arai, H. P., and D. R. Mudry. 1983. Protozoan and metazoan parasites of fishes from the headwaters of the Parsnip and McGregor rivers, British Columbia: a study of possible parasite transfaunation. Can. J. Fish. Aquat. Sci. 40: 1676–1684.

Backiel, T. 1985. Fall of migratory fish populations and changes in commercial fisheries in impounded rivers in Poland, p. 28–41. *In* J. S. Alabaster [ed.] Habitat Modifications and Freshwater Fisheries. Butterworth, London.

Bernacsek, G. M. 1984. Dam design and operation to optimize fish production in impounded river basins. CIFA Technical Paper T-II, FAO, Rome. 98 p.

Biette, R. M., G. A. Goodchild, S. J. Nepszy. 1989. Science Transfer Networks for large river management, p. 600–606. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Binns, N. A., and F. M. Eiserman. 1979. Quantification of fluvial trout habitat in Wyoming. Trans. Amer. Fisheries Soc. 108(3): 215–28.

Bishop, K. A., and J. D. Bell. 1978. Observations on the fish fauna below Tallowa Dam during flow stoppages. J. Mar. Freshw. Res. 29: 543–549.

Biswas, A. K. [ed.] 1983. Long-distance Water Transfer. Tycooly Int., Oxford. 416 p.

Bodaly, R. A., R. E. Hecky, and R. J. P. Fudge. 1984a. Increases in fish mercury levels in lakes flooded by the Churchill River diversion, northern Manitoba. Can. J. Fish. Aquat. Sci. 41: 682–691.

Bodaly, R. A., T. W. D. Johnson, R. J. P. Fudge, and J. W. Clayton. 1984b. Collapse of the lake whitefish (*Coregonus clupeaformis*) fishery in southern Indian Lake, Manitoba, following lake impoundment and river diversion. Can. J. Fish. Aquat. Sci. 41: 692–700.

Bodi, F. L. 1985. Ferc and the fish, p. 20–24. *In* F. W. R. Olson, G. White, and R. H. Hamre [ed.] Small Hydropower and Fisheries. Am. Fish. Soc. Bethesda, MD.

Bowman, M. L., and S. B. Weisberg. 1985. Use of multiple unequally sized turbines to reduce flow fluctuations below hydroelectric dams, p. 390–394. *In* F. W. Olson, R. G. White, and R. H. Hamre [ed.] Small hydropower and fisheries. Am. Fish. Soc. Bethesda, MD.

Burt, D. W., and J. H. Mundie. 1986. Case histories of regulated stream flow and its effect on salmonid populations. Can. Tech. Rep. Fish Aquat. Sci. 1477: 98 p.

Chittenden, M. E. 1971. Status of the striped bass (*Morone saxitilis*) in the Delaware River. Chesapeake Sci. 12: 131–136.

Cushman, R. M. 1985. Review of ecological effects of rapidly varying flows downstream from hydro-electric facilities. N. Am. J. Fish. Manage. 5: 330–339.

Davies, B. R., and K. F. Walker [ed.]. 1986. The Ecology of River Systems. Junk, Dordrecht. 793 p.

Decamps, H. 1984. Towards a landscape ecology of river valleys, p. 163–178. *In* J. H. Cooler and F. B. Golley [ed.] Trends in ecological research for 1980's. Plenum, New York, NY.

Decamps, H., J. Capblanq, H. Casanova, and J. M. Tourenq. 1979. Hydrobiology of some regulated rivers in the southwest of France, p. 273–288. *In* J. V. Ward and J. A. Stanford [ed.] The ecology of regulated rivers. Plenum, New York, NY.

Din, S. H. S. 1977. Effects of the Aswan High Dam on the Nile flood on the estuarine and coastal circulation pattern along the Meditarranean Egyptian coast. Limno. Oceanogr. 22(2): 194–207.

EIFAC. 1982. Report of the Symposium on stock enhancement in the management of freshwater fisheries. EIFAC Tech. Rep. 42. FAO, Rome. 43 p.

1984. Documents presented at the symposium on stock enhancement in the management of freshwater fisheries. EIFAC Tech. Rep. 42, Supplements 1 and 2. FAO, Rome. 2 vol.

Gardiner, J. L. 1988. Environmentally sound river engineering — examples from the Thames catchment. Regulated Rivers 2(3): 445–469.

Golubev, G. N., and A. K. Biswas. 1985. Large scale water transfers: emerging environmental and social experiences. Tycooly, Oxford. 158 p.

Gore, J. A., and R. D. Judy. 1981. Predictive models of benthic macroinvertebrate density for use in instream flow studies and regulated flow management. Can. J. Fish. Aquat. Sci. 38: 1363–70.

Gore, J. A., and G. E. Petts [ed.] 1989. Advances in regulated river ecology. CRC Press, Boca Raton, Florida. (In press).

Gras, R., and J. P. Albignat. 1985. The impact of hydraulic works on water-quality. International Water Power and Dam Construction 37(4): 45–48.

1985. The impact of hydraulic works on water-quality. Part Two. International Water Power and Dam Construction 37(5): 41-46.

IBP 1978. Methods for assessment of fish production in fresh waters. International Biological Programme Handbook No. 3, 3rd Edition, Blackwell, Oxford. 365 p.

JUNK, W. J. 1984. Ecology, fisheries, and fish culture in Amazonia, p. 443–476. *In* H. Sioli [ed.] The Amazon. Junk, Dordrecht.

LARSON, D. Q. 1984. Effectiveness of reservoir releases to provide river temperatures and flows optimal for Pacific Salmon and steelhead trout in the Pacific Northwest, USA, p. 365–386. *In* A. Lillenhamer, and S. J. Saltveit [ed.] Regulated Rivers. Oslo, Universitetsforlaget As.

MATHUR, D., W. H. BASON, E. J. PURDY, AND C. A. SILVER. 1985. A critique of the Instream Flow Incremental Methodology. Can. J. Fish Aquat. Sci. 42: 825–831.

MORGENSEN, S. A. 1984. The effects of water level fluctuations on the spawning success of largemouth bass (*Micropterus salmoides*) in Lake Mead, p. 563–578. *In* V. D. Adams, and V. A. Lamarra [ed.] Aquatic Resources Management of the Colorado River Ecosystem. Ann Arbor, MI.

MUIR, J. F., AND R. J. ROBERTS. 1982. Recent advances in aquaculture. Croom Helm, London. 453 p.

NEWBURY, R. W., G. K. MCCULLOUGH, AND R. E. HECKY. 1984. The southern Indian Lake impoundment and Churchill River Diversion. Can. J. Fish. Aquat. Sci. 41: 548–557.

NORTH, R. M., L. B. DWORSKY, AND D. J. ALLEE. 1980. Unified river basin management. American Water Resources Association, Minneapolis. 654 p.

ORSBORN, J. F., AND C. H. ALLMAN. 1976. Instream flow needs. Am. Fish. Soc. Bethesda, MD. 2 vol.

ORTH, D. J. 1987. Ecological considerations in the development and application of instream flow-habitat models. Regulated Rivers, 1(2): 171–182.

PELZ, G. R. 1985. Fischbewgungen uber verschiedenartige Fischpasse am Beispiel der Mosel, Cour. Forsch.- Inst. Senckenberg, Frankfurt *a.M.* 190 p.

PETTERSON, S., AND P. MELLQUIST. 1984. The effect of supersaturated water at Norwegian water power plants on fish mortality, p. 81–86. *In* A. Lillehammer and S. J. Saltveit [ed.] Regulated Rivers. Universitetsforlaget As. Oslo.

PETTS, G. E. 1984. Impounded Rivers. Wiley, Chichester. 326 p.

1987. Ecological management of European rivers: a European perspective. Regulated Rivers, 1(4): 363–369.

1988. Time-scales for ecological change in regulated rivers, p. 257–266. *In* J. F. Craig and J. B. Kemper [ed.] Regulated streams: advances in ecology. Plenum, New York, NY.

PETTS, G. E., AND R. WOOD. 1988. River regulation in the United Kingdom. Special Issue of Regulated Rivers 2(3): 199–478.

PETTS, G. E., A. L. ROUX, AND H. MOLLER. 1989. Historical changes of large alluvial rivers in western Europe. Wiley, Chichester. 360 p.

SCHNICK, R. A., J. C. MORTON, J. C. MICHALSKI, AND J. T. BEALL. 1982. Mitigation and enhancement techniques for the upper Mississippi River system and other large river systems. U.S. Dep. of the Interior. Fish and Wild. Serv., Washington. Resour. Publ. 149. 714 p.

SCUDDER, T., AND T. CONNELLY. 1985. Management systems for riverine fisheries. Fish. Tech. Pap. 263, FAO, Rome. 85 p.

SEDELL, J. R., AND K. J. LUCHESSA. 1982. Using the historical record as an aid to salmonid habitat enhancement, p. 210–223. *In* N. Armantout [ed.] Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Portland, OR.

SWALES, S., AND K. O'HARA. 1980. Instream habitat improvement devices and their use in freshwater fisheries management. J. Environ. Manage. 10: 167–179.

WALESH, S. G. 1973. Floodland management: the environmental corridor concept, p. 105–112. *In* Hydraulic Engineering and Environment, American Society of Civil Engineers, New York, NY.

WARD, J. V., AND J. A. STANFORD. 1979. The ecology of regulated rivers. Plenum, New York, NY. 398 p.

WELCHE, E. B. 1980. Ecological effects of waste water. Cambridge University Press, Cambridge, UK. 337 p.

WEISBERG, S. B., AND V. A. LOTRICH. 1986. Food limitation of a Delaware salt marsh population of the mummichog (*Fundulus heteroclitus* L.). Oceologia 68: 168–173.

WELCOMME, R. L. 1979. The fisheries ecology of floodplain rivers. Longman, London. 317 p.

1985. River fisheries. Fish Tech. Pap. 262. FAO, Rome. 330 p.

WENGERT, N. 1980. A critical review of the river basin as a focus for resources planning, development, and management, p. 9–27. *In* R. M. North, L. B. Dworsky and D. J. Allee [ed.] Unified River Basin Management. American Water Resources Association, Minneapolis.

WESCHE, T. A., AND P. A. RECHARD. 1980. A Summary of Instream Flow Methods for Fisheries and Related Needs. Water Research Institute. Laramie, Wyoming, USA. Eisenhower Consortium Bull. 9: 122 p.

WHITE, R. J., H. T. KIM, AND J. S. KIM. 1985. PCB's in striped bass collected from the Hudson River, New York, during Fall 1981. Bull. Environ. Contam. Toxic. 34: 883–889.

WHITTON, B. A. 1984. The Ecology of European Rivers. Blackwell Sci., Oxford. 550 p.

WRIGHT, J. F., AND A. D. BERRIE. 1987. Ecological effects on groundwater pumping and a natural drought on the upper reaches of a chalk stream. Regulated Rivers 1(2): 145–160.

WRIGHT, K. R., AND R. M. WRIGHT. 1985. Instream water rights: impact on small hydroelectric plants, p. 327–332. *In* F. W. Olson, R. G. White, and R. H. Hamre [ed.] Small hydropower and fisheries. Am. Fish. Soc. Bethesda, MD.

Sociological Perspectives on Large River Management: A Framework for Application of Optimum Yield

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Abstract

MALVESTUTO, S. P. 1989. Sociological perspectives on large river management: a framework for application of optimum yield, p. 589–599. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

A general conceptual structure for the formal incorporation of biosocioeconomic issues (social accounts) into fishery management on large rivers was conceived by the sociocultural synthesis group at the International Large River Symposium. The four primary social accounts identified were ecosystem health, human nutrition, sociocultural values and economic values. Ecosystem health addresses the degradation of riverine ecosystems by man with associated loss of ecological value. It is suggested that ecological value be most readily evaluated by consideration of the self-organizing features of riverine ecosystems. The nutritional account emphasizes the nutritional contribution of fish to the human diet, a critical social endpoint in many parts of the world. The sociocultural account incorporates all social values that cannot be measured nutritionally, or valued with money. Important sociocultural elements are social structure of the fishery, employment, family ties with fishing, and attitudes affecting fishing behavior. The economic account deals with money. Economic elements relevant to fishery management are net profits associated with fishing, fishing trip expenditures, the viability of support businesses, and the economic importance of fishing to families.

This conceptual structure suggests that fishery management traditions be expanded substantially. This expansion can be considered within the framework of optimum yield (OY). Attainment of OY will entail that research and management objectives, data collection techniques, analytical methods, management strategies, and evaluation of management response, all be modified to incorporate social accounts. This process will necessitate the restructuring of current management institutions and the creative application of participatory, community-based management schemes.

Résumé

MALVESTUTO, S. P. 1989. Sociological perspectives on large river management: a framework for application of optimum yield, p. 589–599. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Le groupe de synthèse socioculturelle a conçu, à l'occasion du colloque international sur les grands cours d'eau, une structure conceptuelle générale pour l'intégration systématique des questions biosocioéconomiques (bilans sociaux) à la gestion des pêches dans les grands cours d'eau. Les quatre bilans sociaux principaux qui ont été identifiés sont les suivants : la santé de l'écosystème, l'alimentation des humains, les valeurs socioculturelles et les valeurs économiques. Le bilan relatif à la santé de l'écosystème porte sur la dégradation des écosystèmes riverains attribuable à l'homme, et sur la perte de valeur écologique qui lui est associée. On pense qu'il est plus facile d'évaluer la valeur écologique en étudiant les caractéristiques de la structure autonome des écosystèmes riverains. Le bilan relatif à l'alimentation met l'accent sur la contribution du poisson au régime alimentaire des humains, élément social ultime et essentiel dans bon nombre de régions du globe. Le bilan socioculturel englobe toutes les valeurs sociales qui ne peuvent être évaluées sur le plan de l'alimentation, ou assorties d'une valeur monétaire. La structure sociale du secteur de la pêche, l'emploi, les rapports entre les familles et ce secteur, et les attitudes qui influent sur le comportement dans le cadre de cette activité sont des éléments socioculturels importants. Le bilan économique conserve les données monétaires. Les bénéfices nets associés à la pêche, les dépenses engagées dans le cadre des sorties de pêche, la rentabilité des entreprises connexes, et l'importance économique de la pêche pour les familles constituent les éléments économiques pertinents à la gestion de cette activité.

Selon cette structure conceptuelle, il faudrait développer substantiellement la gestion traditionnelle des pêches, que l'on pourrait envisager dans le cadre du rendement optimum. L'atteinte de ce rendement entraînera la modification de l'ensemble des objectifs en matière de gestion et de recherche, des techniques de cueillette des données, des méthodes d'analyse, des stratégies de gestion et des modes d'évaluation des réactions des mécanismes de gestion, pour intégrer les bilans sociaux. Ce processus exigera la restructuration des institutions de gestion courantes et la mise en œuvre originale de régimes de gestion fondés sur la participation et sur la collectivité.

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The perspectives on large river management presented here stem largely from ideas generated by the sociocultural synthesis group formed at the International Large River Symposium (Dodge 1989). I have taken the liberty to expand on these concepts within the framework of my own experience as a fisheries biologist, hopefully without losing sight of the overall group goal. Though not explicitly stated at the outset, our goal became the development of a conceptual framework for identification and eventual application of social values to the management of riverine ecosystems and associated fisheries.

Two precepts guided the flow of ideas: (1) rivers have intrinsic value, i.e., value in and of themselves, independent of human benefits that may be derived therefrom; and (2) there are explicit and implicit social and economic values associated with rivers affected by human processes. It is the enhancement of these social and economic values that justifies our fishery management decisions, as well as larger scale decisions concerning modifications of riverine ecosystems.

It is safe to say that presently fisheries managers have little idea what socioeconomic elements are important, let alone how to measure them and to incorporate them into decision-making. It is rare, then, that information is collected other than traditional fishery biology descriptors (effort, catch, CPUE, species composition, etc.). Collection of economic data usually is limited and often inappropriate for management purposes.

An initial broad categorization of social values, or social accounts (as I will frequently refer to them here) relevant to fishery management issues, as well as to general development issues on large rivers, is as follows: (1) value (health) of the ecosystem; (2) nutritional or dietary value of harvest consumed; (3) sociocultural values; and (4) economic values.

For any particular river, the first account would reflect the biological health, or well-being, of the aquatic environment. A biologically degraded environment would have less ecological value than an unmodified environment. A more complex ecosystem, as determined by habitat and species diversity, or a more biologically unique ecosystem, might contain more intrinsic ecological value than simpler, or more common, riverine assemblages.

The second account, nutritional value, would measure the dietary contribution of fish, or other organisms harvested from rivers, to the nutritional well-being of people consuming the products. The focus would be on the contribution of these foods to intake of calories, proteins and nutrients that influence human health.

The third account, sociocultural values, is extremely general and meant to include all societal values that cannot be quantified nutritionally or economically. If dollar signs can be assigned, then other measures of value to society might also be derived to supplement the economic measures for fisheries management purposes.

The fourth account incorporates the traditional economic values that derive from the various monetary analyses that might be applied to fisheries enterprises, either commercial, recreational or subsistence.

This synthesis paper, then, attempts to sketch a useful framework within which a sociological method for fishery assessment and management might be derived.The framework is not necessarily all inclusive as is that of Talhelm and Libby (1987) whose 'total value framework' classifies all social values as either ''held'' (basic human values) or ''assigned'' (market values). As is evident above, the conceptual model presented here seeks to provide a relatively comprehensive structure for addressing social values. The presentation to follow, however, strives more to identify key elements within the structure; that is, elements with utility from a fishery managers standpoint. With this in mind, the orientation is more toward assessment and management of regional, local, or resource-specific situations, rather than toward provincial, state, national, or other macro levels.

As applied more specifically to fisheries science, the focus here is on definition of a more meaningful conceptual framework for the application of optimum yield, or OY. By definition, OY is to embody relevant biological, economic and social factors with respect to fisheries management decision-making. Fisheries sociologists have found OY to be a convenient conceptual structure for development of sociological priorities for fisheries research and management (Vanderpool 1986).

Application of Social Accounts to Fisheries Management

The application of social values to fisheries management in large rivers might be explored effectively by examination of issues that must be addressed if such values are to be used by those responsible for making decisions concerning river resource use. Figure 1 offers a structured process for development of fisheries management programs. In the sections to follow, I will endeavor to discuss each of the four social accounts identified above in relation to the development process shown in Fig. 1. The linkage will allow fisheries managers to conceptualize better the modifications in our current thinking that are necessary if we truly are to attain OY from our aquatic resources.

Development Stage #1: Setting Objectives

Most fisheries management proposals that I have read openly state that the ultimate goal of the project is to increase benefits to people. The specific objectives, however, usually only address traditional fishery management endpoints, such as to increase fishing success for particular species, to insure large sizes of fish in the harvest, to increase or decrease rates of exploitation, or to enhance reproduction and recruitment. In the majority of cases, whether enhanced benefits to people truly are realized via the traditional management objectives, cannot be evaluated — social accounts, though implied, are not explicitly addressed. Fisheries managers have found it convenient to assume that ''good'' biology translates into positive social benefits.

Our traditional array of objectives must be expanded, then, to include observation and measurement of things relevant to the four accounts listed above. Some current perspectives follow.

Ecosystem Health

It is reasonable that the healthiest ecosystems, those with the highest intrinsic value, would be natural ecosystems under no human stresses. Ecosystem health could be viewed

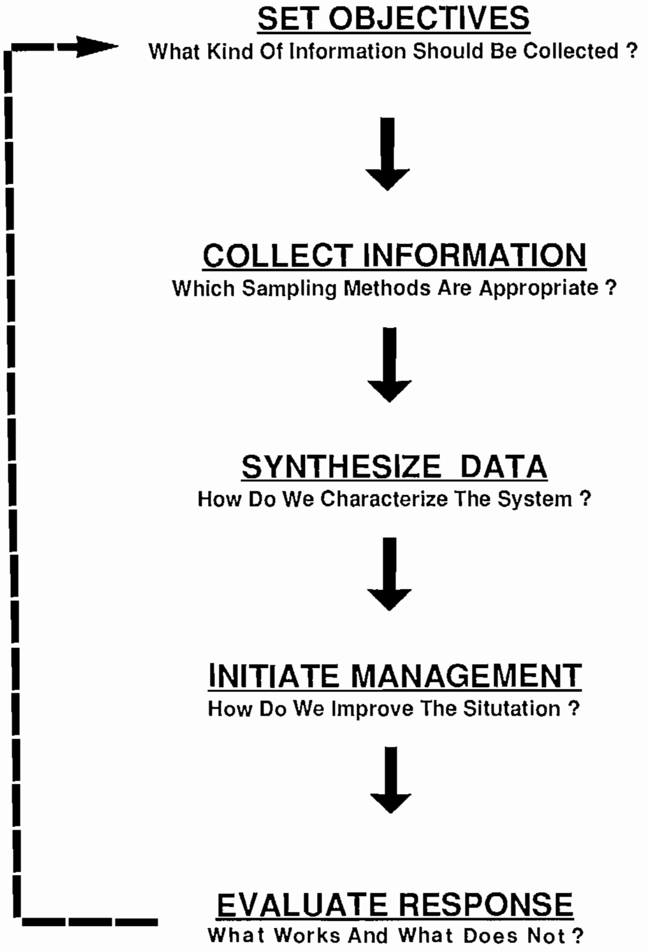

FIG 1. Development process for fishery management. Each stage must be expanded beyond traditional boundaries to address social accounts for optimum management. The major feed-back loop suggests a formalized experimental approach to development of management options.

as progressively deteriorating as ecosystem states deviated more and more from the natural condition. Regier et al. (1989) present a taxonomy of stresses that affect aquatic ecosystems, progressing from natural background processes, on the unstressed side, to restructuring basin morphometry and the introduction of exotics, on the highly stressed side. This sort of classification alone, applied to a particular river, would give an indication of probable deviation of the present condition from the natural state.

Given that the natural state of an ecosystem has been described using some set of criteria, or can be reconstructed in some manner as through comparison with seemingly similar unstressed habitats, then changes from the natural condition can be evaluated by comparing current values of criteria variables with natural state values. Categories of criteria variables might include: water quality, quantity and timing of flow; floral and faunal diversity and productivity of key species, or groups of functionally related species; and changes in basin morphometry and aquatic habitat.

Most of our traditional fishery descriptors are associated with biological aspects of aquatic ecosystems, primarily fish stocks, and can be classified as indicators of ecosystem health, though typically not viewed as such. Harvest (rate of exploitation), CPUE (stock density), species composition, length/age structures, growth, recruitment, etc., all characterize the dynamics of fish populations and typically are used to establish the effects of exploitation on fish resources, i.e. to establish levels of human stress on ecosystems.

The health of an ecosystem might be most readily evaluated by considering its large scale integration rather than to compartmentalize the ecosystem drastically and then to reintegrate its parts. Thus, Regier et al. (1989) stress that it may be more useful to look at the self-organizing features of ecosystems, with an emphasis on information contained within, rather than on enery flow-through. With this perspective, the behaviors of reproduction and predation become important and particular features of ecosystems stand out as points of management concern. For example, the ''centers of organization'' of Regier et al. (1989) and the ''hot spots'' of Sedell et al. (1989), refer to locales on large rivers associated with predator–prey and reproductive behaviors that are critical to the successful continuance of the more valuable organisms. These locales tend to be deposits of large trees or rocks, vegetation beds, and flood plain areas easily identifiable by resource managers. The linkage from ecosystem health → man-induced stresses → management, is readily established.

If river basins, or portions thereof, could be classified according to stages of development, or progressive stages of stress as per the taxonomy of Regier et al. (1989), then perhaps the importance of particular social values could be related to the degree of population growth and industrialization, and thus also likely to the degree of devaluation of aquatic ecosystems. The existence of these types of relationships would allow some degree of forecasting of the importance of particular social values in specific circumstances as a guide to developing management and evaluation programs. This approach might provide a firmer conceptual basis for meaningful application of OY to a variety of circumstances, from subsistence fisheries on untouched rivers, to urban recreational fisheries on highly modified systems.

Preliminary exploration by the synthesis group of possible associations between river morphometry (length, basin area, latitude), fish diversity (number of species), commercial fish yields ($kg \cdot ha^{-1}$), and indirect measures of development and degradation (basin population size, per capita GNP, number of dams), showed that many basic statistics are unknown, or not reported in a convenient or standardized fashion. On a world-wide basis, indices of river development and degradation were sparse and, even in Dodge (1989), when studies noted pollution and river modifications, few provided absolute quantification. A standard set of indicators of ecosystem health would aid the consistency of data collection, the compatibility of findings, and the interpretation of nutritional, sociocultural and economic consequences of human manipulation of river ecosystems.

Nutritional Value

A common focus of fisheries managers is on the harvest of fish. The value of the harvest as food is readily acknowledged, but estimates of harvest typically are used to evaluate the effects of fishing on important stocks, or to place economic value on the fish being removed from the system. The actual nutritional contribution of fish to the diet is rarely evaluated as such, although enhanced nutritional well-being is certainly a potential human benefit derived from any particular fishery.

In its most elaborate sense, nutritional value could be assessed by determining the contribution of fish, along with other foods eaten, to calories, proteins, and essential vitamins and minerals in the diets of people eating fish from a particular resource. Dietary deficiences can be evaluated relative to published values of standard daily requirements for acceptable nutritional well-being for the segment of society under consideration. The importance of the nutritional account could be assessed by determining if the presence of fish in the diet enhanced the levels of any limiting elements (elements in the diet below the acceptable in-take standards). Thus, if all dietary requirements were satisfied without the presence of fish, then the nutritional account would have zero value — there would be no nutritional benefit associated with the resource. This likely is the general case with anglers in the United States. It is easy to envision, however, that if the human group of concern was children of fishing families in the Sahelian region of West Africa, then the nutritional account could be extremely important and should be formally incorporated into assessment and development decisions.

The potential importance of the nutritional account would immediately stand-out if gross indications of dietary deficiencies were apparent, e.g., high infant mortality, low per capita in-take of proteins and calories. Thus, there might be country-wide or regional indicators of the importance of fish in the diet which could justify that certain management and development programs be implemented. Where the nutritional justification for fisheries development is strong, however, so is the need for good documentation of the nutritional status of the target population and the contribution of fish to the diet. Only in this manner can the nutritional benefits of any management or development action be evaluated.

Sociocultural Values

Sociocultural elements are those that do not fall into the nutritional realm or those that cannot meaningfully be valued with money. Major sociocultural areas that seem relevant to fisheries management on a world-wide basis are: (1) social structures of fisheries; (2) employment; (3) family ties with fishing; and (4) attitudes affecting fishing behavior. These four areas are relatively broad and I will treat each in more detail.

(1) Social structure of fisheries. The social structure of a fishery can be taken as a gross organizational description of the system under study — what are the system components (who are the players), and how are they linked? To a large degree, this might be addressed by mapping the flow of fish through the system, from harvest to consumption, with identification of the sectors through which the fish pass, e.g., harvesting → distribution → processing → marketing → consumption (Fig. 2).

In the recreational setting, the harvester, distributor, processor and consumer may be simply the angler, immediate family and fishing friends. Other social organizations tied closely to fishing and to the family (fishing clubs, conservation groups) might also be part of the chain of immediate social benefits (Fig. 2). A logical sociological orientation to assessment in this situation would be to focus on individual anglers, their households and relevant social groups in the community, as primary beneficiaries of the fish resource and also as loci for information exchange and research.

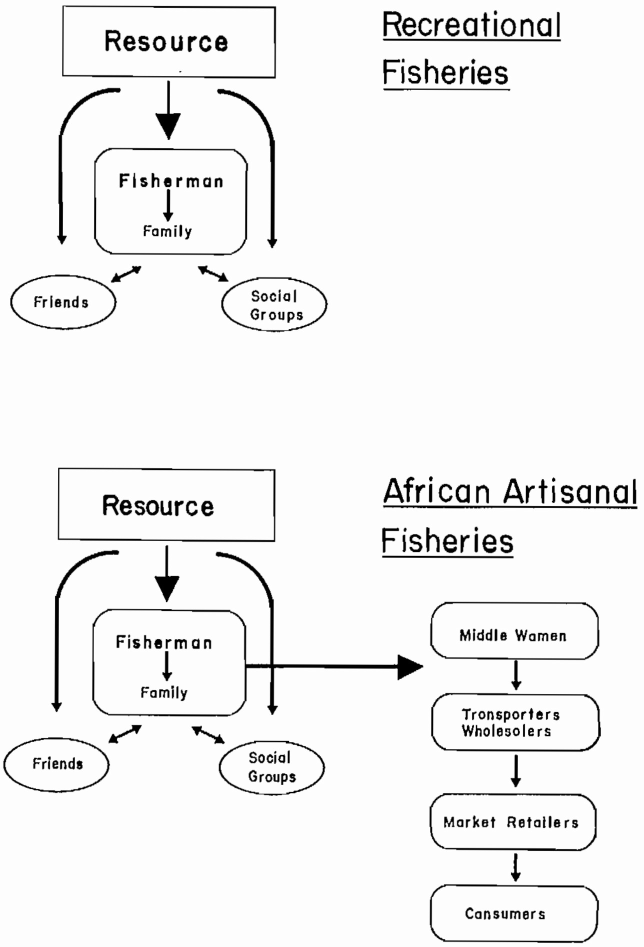

FIG 2. Social sector diagrams developed by tracing the flow of fish (arrows) through production, processing, marketing and consumption components of typical recreational and African artisanal fisheries. Diagrams allow identification of important human sectors for collection of social data. Models are aimed at localized, resource-specific assessment, and conceptualize the fisherman-family as primary users of the resource.

Taking a more complex example, an artisanal riverine fishery in Africa might be organized as family harvesters who sell their catch riverside to a middle woman, who in turn sells her purchases to a transporter/wholesaler, who then sells the fish to a market retailer, where they are finally bought by consumers. Parallel to this flow of fish, there is a direct flow into the fishing households for consumption (Fig. 2). This model, with slight modification, might fit any localized, small-scale commercial fishery. On-the-one-hand, there are sociocultural benefits being derived at each level in the marketing chain and a full understanding of the operation of the fishery should entail gathering information at each level. On-the-other-hand, there is a more localized focus, based on the flow of fish into households, with other associated community end-points, not unlike the social organization of the recreational fishing experience.

The diagrams in Fig. 2, via the flow of fish, trace the flow of social benefits within the structure of the fishery. Mapping helps to identify human sectors where important sociocultural values likely reside. Once important social sectors have been identified, then it is desirable to describe each in more detail, particularly ethnographically. Who are the people involved in these social assemblages? How many? Ethnic backgrounds? Sexes and ages? Per capita statistics on income levels and literacy rates can help to provide a more general classification of the social climate under consideration. Thus, Pollnac (1985) sets a broad sociological structure for West African coastal small-scale fisheries by reviewing the GNP, percent literacy of people over 15 years old, life expectancy, infant mortality, density of roads, percent of toal population urbanized, and percent average annual growth in urban areas.

(2) Employment. In its basic form, employment is the number of people employed by the fishing industry, or sectors thereof, and is another general indicator of social value. Although anglers are not necessarily employed by the recreational fishing industry, their participation, measured as fishing trips for example, gives a gross idea of the magnitude and pervasiveness of the social benefits being derived by those using recreational resources.

In a fuller sense, employment should consider the social structure of work, ownership rights, money exchange systems, as well as alternative employment opportunities. Relevant questions here might be: Who owns what and who works for whom? What rights do owners of boats, facilities and other equipment have with respect to controlling employment and money distribution? What are the rules by which money is distributed — by whom, form, timing? What is the mix of full-time and part-time fishermen? What is the allocation of time spent in various money-making activities? Where could people work if not occupied in the fishery? How many people could the job alternatives employ? Are there roles for women as independent wage earners?

(3) Family ties with fishing. Although the individual fisherman and immediate family may take on various levels of importance depending on the fishery (see Fig. 2), it would seem that the family unit should be a primary focus for documentation of sociocultural benefits derived from fisheries. These are the people that will be tied most closely to a specific resource in other than economic ways. Some specific sociocultural issues relevant here are:

(a) How are kinship relations and family roles associated with fishing? Are crews, boat owners, middlemen, processors, etc., related to one another? Do household members have different work roles and responsibilities in the fishery? Are apprenticeships and family ownerships traditional?

(b) How does the temporal, spatial and economic nature of fishing as an activity affect intrafamily relationships? What are effects of fishing on time spent among family members and on family stress in general? Who earns the money and who allocates spending in the household? Are there particular benefits derived from women as wage earners, e.g., better nutrition of small children?

(c) What are the effects of the fishery on relationships between families? Does the fishery bring families together? Is there interfamily sharing of resources (equipment, facilities) for operation of the fishery, or sharing of the harvest? Are there larger, fishery-related affiliations of families where benefits are derived (work efficiency, protecting vested interests in the fish resource)?

(4) Attitudes affecting fishing behavior. The fourth major component of the sociocultural account addresses attitudes. Attitudes are taken here to represent an expression of values and beliefs. Attitudes govern what people want to receive from fishing, as well as how they undertake the activity (Harris 1986). For the sake of classification and discussion, it is taken that attitudes have a bearing on the following: expectations, satisfaction, behavior, perceptions and receptivity. With respect to fisheries assessment, the following questions are relevant: What do people want from the resource? What is important to them? Are their expectations being met? Are they satisfied with their involvement in the fishery (be it harvester, processor, retailer, etc.)? What constitutes good fishing (acceptable practices) vs bad fishing? What kind of behaviors have been detrimental to the resource? Are there beliefs or traditions (religious or otherwise) that restrict resource utilization? Who is restricted, how, when and where? How do people perceive regulatory, enforcement and management authorities? Do they have faith in these authorities? What are the people's opinions of various regulations and management plans? Do they have an understanding of the reasons for these plans? What do the people feel would improve the resource? Are people willing to cooperate/learn/teach? Are they receptive to innovation and change? Attitudes can diverge strongly across social sectors (Fig. 2), particularly if composed of different ethnic, religious, or other socioeconomic groupings.

Economic Values

Overall, the economic account deals with money. Key economic elements can be identified using a money flow diagram. Figure 3 shows money flow diagrams for the same two fisheries depicted earlier in Fig 2. In its simplest from, a money flow diagram identifies places where money exchanges hands. Note how much different in structure the social (Fig. 2) and economic (Fig. 3) diagrams are for the recreational fishery — the money flow diagram identifies a completely different network of players. It is clear that the flow of money is directed from anglers into support businesses (and out of support businesses into larger manufacturing units not shown on the diagram). The sport fisherman, by definition, earns no money by fishing or by selling fish.

The differences in the social and economic patterns are not as marked with respect to the African artisanal fishery. Given an emphasis on the commercialization of fish, social sectors are also places of money exchange. Primary economic activity revolves around the sale of harvested fish as they move throught the market system. Unlike anglers, commercial fishermen make money from their interaction with the resource; however, both groups must give money to businesses in exchange for variable and durable fishing necessities. Both groups exhibit similar social and economic patterns with respect to the family and immediate community (Fig. 2 and 3).

For a given fishery, once money exchanges have been identified, there may be several ways of describing economic value. With reference to fisheries management, some important emphases should be: (1) net profits; (2) expendi-

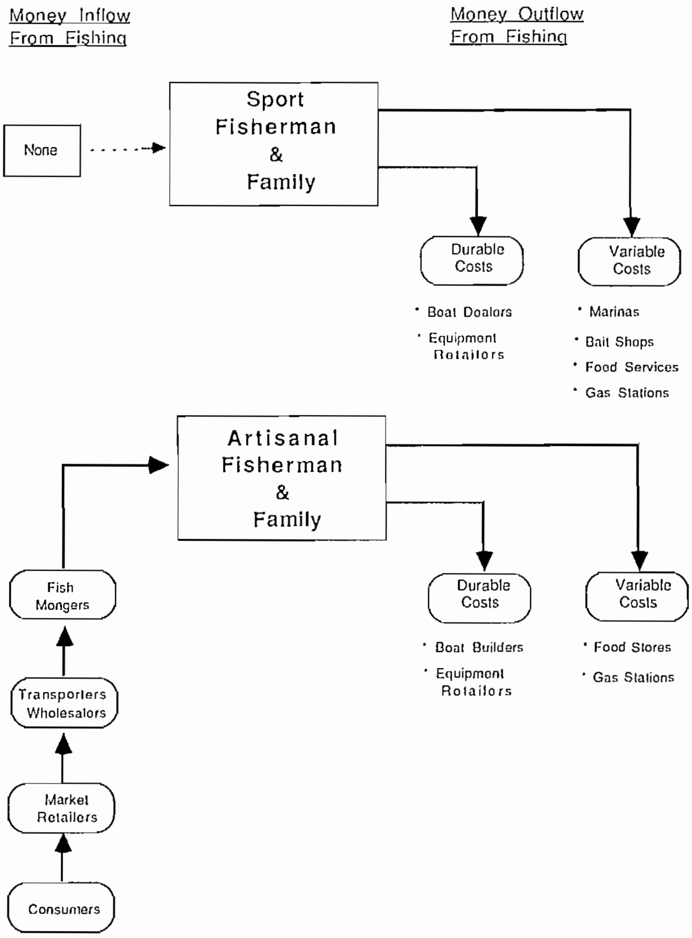

FIG 3. Money flow diagrams tracing the flow of cash (arrows) through typical recreational and African artisanal fish systems. Diagrams aid identification of social sectors of economic activity for data collection and management consideration. Models are aimed at localized, resource-specific management, and conceptualize the fisherman-family as primary users of the resource.

tures and the viability of support businesses; and (3) economic importance of fishing to the household.

(1) Net profits. The most useful measure of economic efficiency is profitability. For any particular enterprise, if profits (revenues minus costs) are positive, then the enterprise is economically viable; the higher the profits, the higher the economic efficiency.

In the commercial fishery setting, evaluating profitability follows traditional lines, where variable and durable costs of fishing can be tallied against gross monetary returns to give either a positive or negative net profit on an annual basis. Profit differentials can vary, however, across socioeconomic sectors (Fig. 2 and 3). In the recreational setting, there is no economic activity directly associated with marketing fish or with rental of the resource (Fig. 3); thus, there are no monetary returns to balance against the costs of fishing, and profit cannot be directly estimated. Willingness to pay for use of a recreational resource, over and above the associated costs of fishing, is taken as the potential profit associated with the fishery. This value is termed consumer's surplus (Palm and Malvestuto 1982; Malvestuto 1983). Obviously, if user fees are involved, then profit can be more traditionally evaluated. Glass and Muth (1987) give a succinct critique of fishery valuation techniques.

(2) Expenditures and support businesses. The money that people spend to catch fish, whether for profit or pleasure, flows to support businesses. Some of these businesses will be tied closely to fishing at a particular location, e.g., local marinas, bait and tackle shops, guide services, equipment and boat dealers. Given more localized resource management objectives, it would be reasonable to focus on the viability of businesses closely tied to particular fish resources as an indication of the importance of the economic benefit derived from the fishery by the community. What businesses are involved with fishing in some way? What portion of the profits associated with these businesses is derived from the fishery? How do profits from fishery-related businesses compare to those of other enterprises in the community?

(3) Economic importance of fishing to the household. Just as there were sociocultural values appropriate to households, there are also economic values which seem most appropriately considered at the household level. What is the contribution of fishing, or fishery-related work, to gross household earnings and discretionary income? How would the economic viability of the household suffer if income from the fishery was lost? Does household use of harvest mitigate food expenses to any degree?

The description of the four social accounts given above was aimed at identification of fishery assessment objectives (stage #1 in Fig. 1) that potentially should be considered if OY is to be purposefully addressed by fisheries managers. These objectives are collated in Table 1 and represent a rudimentary framework for the practical utilization of OY. I have not treated all issues in an equitable manner and there are certainly critical areas that were overlooked. For example, I ignored intrinsic economic values, which include option and existence values (Bishop et al. 1987), because, although they are certainly at the root of policy decisions, they are difficult to estimate in a reliable fashion (Rettig 1987; Glass and Muth 1987). In the same vein, economic input analysis (Martin 1987) is likely too rigorous for the periodic assessments needed by fishery management agencies, especially if other social account data also are collected. However, both of these valuation procedures would be helpful in special circumstances, e.g., important state-national conservation issues (preservation values), or high influx of outside money generated by demand for fishing opportunities (economic impact analysis).

From an applied standpoint, the issue of OY must be artifically limited in some manner if fishery managers are to begin to use the concept in a purposeful way. The array of objectives summarized in Table 1 is an attempt to address stage #1 of the development process depicted in Fig. 1 so that the remaining stages of the process can be explored.

Development Stages 2 and 3: Collection and Synthesis of Information

The social factors identified above represent a subset of the totality of factors contained within the social accounts model. Regardless of the particular subset identified, data must be collected in the field and subjected to qualitative and quantitative analysis for decision-making. The data collection and synthesis methods depend on, and should be tailored, to, the chosen objectives.

TABLE 1. Summarization of objectives relevant to development of social accounts for large river management. The objectives identified represent a rudimentary framework for application of optimum yield (see text for details).

Social Account	Objectives
Ecosystem Health	Develop standard measures of water quality, quantity and timing of flow, floral and faunal diversity and production, and basin morphometry and aquatic habitat. Identify "centers of organization" for managment focus.
Human Nutrition	Determine contribution of fish to the diet by comparing nutritive value of food eaten to recommended daily standards. Do fish contribute to achieving daily requirements of any essential elements?
Sociocultural Values	Describe: (1) Social structure of fishery — players and linkages (social sector diagram); (2) Employment — # people, work structure, money exchange systems, alternate employment opportunities; (3) Family ties with fishing — kinship relations, family roles and intra- and interfamily relationships; (4) Attitudes affecting fishing behavior — what do people expect and what makes them satisfied? How do they perceive the fishery and management institutions? Are people willing to learn/cooperate/teach?
Economic Values	Determine social sectors of money exchange (money flow diagram). Measure net profits, expenditures to support businesses, and economic contribution of fishery to households.

As students of the biological or social sciences we are all familiar with the study methods used in our chosen fields. The transdisciplinary nature of river management dictates that it is the spectrum of these methods that relates to our needs, particularly for the application of OY. I cannot here explore in detail the methodological and analytical issues relevant to the collection of the broad array of social account information. However, some general points should be made. Of major importance is that the fundamental methods for collection of OY data do exist, though adaptations and new approaches certainly will be necessary. The core nutritional and ethnographic survey techniques are based on the same statistical survey methods that fisheries biologists use for creel surveys, catch assessment surveys, angler preference and opinion surveys, and the like, i,e., sample surveys of people (Malvestuto 1983; Smith 1983).

Nutritional assessment technologies can be tailored to the prevalence and severity of the nutritional problem, to the goals of the management program, to the available resources, and to the sociocultural setting (Newton 1983). There are simple indicators of malnutrition that can be used in the field (weight-for-age, height-for-age, weight-for-height and arm circumference, for example) that measure gross nutritional deficiencies (Newton 1983). Twenty-four-hour food recalls can be used to assess food intake, and food tables (which give the nutrient composition of various foods) are available for virtually every part of the world (Food and Agricultural Organization of the United Nations and the United States Department of Health, Education and Welfare). Thus dietary intake, measured as amounts of particular kinds of foods cooked in various ways, can be converted to elemental intake of vitamins, minerals, proteins, carbohydrates, fats, calories, etc.. Thus, dietary contribution to nutritional well-being can be measured.

Ethnographic survey techniques for collection of sociocultural information are based largely on exploration of written histories, collection of oral histories, and observation of participant behavior to obtain knowledge of fishing techniques, terminology, and daily activities. Collection of these types of information will entail elaboration of land-based household and community surveys as fisheries assessment tools, even to the point of living with fishing families to gain first-hand knowledge of important social elements that could weigh heavily in a decision-making context.

Participation by researchers, managers, and community members together to define objectives and to collect data is the basis for empirically-adapted assessment programs that are appropriate to the situation at hand, mutually acceptable to those involved, and open to evaluation and modification for improved benefits to the community. Farming systems research (Shaner et al. 1982) and development sociology (Cernea 1984) are social assessment methods recently applied to agricultural production systems in lesser developed countries. Farming systems research has been conceptually related to fisheries assessment by Sissoko et al. (1985). Rural sociology has long neglected the study of core food production processes and there is a strong need for the development of systematic bodies of sociological know-how fitted to purposeful development intervention (Cernea 1984).

It would be efficient, given the wide-spread use of creel surveys, catch assessment surveys, fishermen opinion surveys, and the like, to take advantage of these on-going efforts for incorporation of social account information. With a fix on the kinds of data that can be valuable for management decisions (Table 1), fisheries biologists can collect certain social data along with traditional fishery data at little extra cost. It is critical that research on development of cost efficient survey options, and on complementary use of different survey techniques, be conducted in a timely manner.

The social sector and money flow diagrams (Fig. 2 and 3, respectively) can be partitioned in any manner to define social and economic universes for data collection. It is most likely true that the harvesters, their families, and the immediate community, are most closely tied nutritionally, socially and economically to the integrity of a particular ecosystem. Thus, for site-specific river management, it is the users of the resource, and those directly dependent on its maintenance, that deserve the immediate focus of researchers and managers. Families were specifically identified as assessment units in the nutritional, sociocultural and economic accounts. Bayley and Petrere (1989) argue for more use of household surveys, and household statistics from general demographic surveys, as effective substitutes for some kinds of on-site interview data. They used annual per capita consumption of fish estimated from household surveys to obtain comparable, but more precise, estimates of fish yields from South American rivers than were possible using traditional landing statistics. Malvestuto and Meredith (1989) used an on-site survey of fishing households to characterize the family economics of the artisanal fishery on the Niger River in Niger, West Africa.

It is not necessarily best for fisheries management purposes to treat data as is traditionally done in the social and economic disciplines. Our analytical techniques must summarize data in ways that are relevant to fisheries management issues and that are clear to fisheries administrators. The integrated collection of social account data will allow for exploration of OY relationships using external analytical approaches (Kerr 1982) and should provide a basis for derivation of more holistic fishery descriptors.

As an example, Malvestuto and Meredith (1989) found that both mean CPUE (measured as daily harvest per canoe), and mean price of fish to harvesters, stayed constant over a 3-year period when the fishery on the Niger River in Niger was going through severe declines in fishing activity and harvest because of long-term drought conditions in the Sahel. Mean CPUE and mean bankside price of fish, then, when taken independently, were not responsive to the large-scale changes in progress during the study. However, when the frequency distribution of CPUE was partitioned according to the mean daily catch needed for a harvester to break-even economically, it was found that the percentage of no-profit days (days when the CPUE was below the mean break-even catch) was sensitive to the observed trends in catch and effort. The new descriptor enabled a better understanding of factors affecting fishermen behavior during this critical period. The percentage of no-profit days is a simple bioeconomic index built on information from a catch assessment survey (frequency distribution of CPUE and bankside price of fish) and on information collected from households (daily revenue from fishing needed to break-even).

Development Stage #4: Management

The identification of program objectives and the subsequent collection and analysis of appropriate data, sets the stage for management (Fig. 1). The array of social assessment objectives summarized in Table 1 necessitates development of an expanded repertoire of sampling and analytical methods, all of which will lead to new orientations and options for fisheries managers. Some perspectives on OY management follow.

As fisheries managers, our major challenge likely will be optimizing the gain in the nutritional, sociocultural and economic accounts in the face of acknowledged loss in value of the ecosystem account. This commonly manifests itself as a tradeoff between conservation and short-term socioeconomic gains (Retting 1987). It can be decided to lower ecosystem value purposefully if social benefits can be increased. Thus, overharvest of piscivores might be accepted if it provided for increased abundance of other valued fishes that previously served as fish food, and were unavailable for harvest by people, so long as net socioeconomic gains were realized via the shift in fish community structure. The tradeoff, however, is increased likelihood of ecosystem destabilization through loss of top predators (Regier et al. 1989). The bottom line, however, is that if social benefits are not identified, measured, and monitored, then the sociological effects of the management option are not known, even if the system shifts biologically as predicted.

The importance of the nutritional account to management will depend on the food value of the harvest. The only paper presented by Dodge (1989) that alluded to nutritional benefit as an important consideration in fishery management was that of Malvestuto and Meredith (1989) on assessment and management of the Niger River fishery in Niger, West Africa. Even in that situation, the issue was not directly addressed, as the authors determined that about 20 % of the fish harvest was funneled directly into fishing households for consumption, but the nutritional benefit associated with this component of the harvest was not measured. It was assumed that 20 % was important for nutritional purposes, but how important, and when, and to which household members, were not determined. It might be likely in that fishery to find that the most critical nutritional contribution of fish to the diet would be for small children under the age of 5 and for lactating mothers during the "hungry season". The hungry season is during, and after, the planting of crops when the people have expended tremendous physical energy and food stores from the last harvest have been exhausted. Seasonal phasing of fishing restrictions in accordance with nutritional needs might be a positive management option in these circumstances.

In the southeastern United States along the lower Tombigbee River, I estimated that from 2 000 to 6 000 low income families bought fish directly from commercial fishermen peddling their harvests from door-to-door in rural, riverine communities (unpublished). The likely importance of the nutritional account was evident in that study, but the actual nutritional benefit at the household level was not measured. Restrictive gear regulations against small-scale commercial fishermen in this region, as for example might occur if politically influential sport fishing groups felt that commercial gear was causing unwanted mortality of game fishes, could decrease nutritional and economic benefits to needy families who may have no other way of regaining the loss. It is certain that there are many localized situations in North America where the value of the nutritional account is high, but presently goes unaccounted (Matlock et al. 1988). The critical aspect for managers is to avoid making regulatory decisions that adversely affect nutritional benefits to people.

It is clear from the literature that increased efficiency of the production component of a food production system (as is the focus of our traditional fishery management approaches) does not necessarily equate to increased nutritional well being of people. There are many cases of negative nutritional effects because of socioeconomic contingencies that disrupted the "more production = better nutrition" equation. Lunven (1983), who reviewed six case histories involving negative nutritional benefits, concluded that increased food production did not improve nutrition because social and economic situations in the project areas were not understood, because the increased production was not reaching the people who were really in nutritional need, and because of the constant problems associated with credit schemes, cooperatives, and other program decisions that brought unpredictable complications. Thus, the sociocultural atmosphere is critical to the success of food production (fish harvest) when measured relative to nutritional benefit. In this respect, the societal role of women as wage earners and providers of nutrition in the household becomes important (Savane 1982).

The actualization of OY will entail more than incorporation of social accounts into management decisions. The most promising managment approaches will effectively integrate administrative agencies and may actually strive to restructure institutional systems. As Retting (1987) points out, institutional changes will affect both public and private costs and little attention has been paid to measuring these costs under various management schemes. Much of the future emphasis of fisheries sociologists will be on territoriality and property rights, the effects of fisheries policy on organization and structure of fisheries, and on the role of sociologists in the policy preocess (Bailey et al. 1986).

The perceived benefit from sociologically sensitive approaches to development, as embodied in farming systems research, developmental sociology, and the like, is that the beneficiaries of the management program, the people, become directly involved in the development, planning, implementation and evaluation of the program, thus increasing the probability of success. Inherent in this philosophy is that the best strategies for development and management should stem from localized, community-based, institutional structures which are able to protect the vested interests of the primary resource users and to exercise the most influence over the behavior of the people — seemingly essential elements for successful management. This orientation is well suited to our OY concerns, whether the application be recreational fisheries in North America or subsistence fisheries in the Amazon River basin.

The restructuring of fisheries management institutions strikes at the heart of our values and beliefs, the social ethics which govern our interactions with fish resources. The issue has taken form in recent literature as a critical evaluation of the characteristics of common property, open-access fisheries (Berkes 1985) and as an exploration of systems of fishing rights and allocation of fish resources (Regier and Grima 1985). Berkes (1985), in an analysis of factors associated with the occurrence of the tragedy of the commons (Hardin 1968), concluded that fishing communities that have been able to avoid the tragedy are those with participatory systems of fishery management which are adapted to local social and economic contingencies. The author characterizes situations in which the tragedy will most likely occur as those where there is loss of community control over the resource in association with commercialization of the fishery, which commonly occurres in conjunction with rapid population growth and technology change. Malvestuto and Meredith (1989) recommended formation of community-based fishing organizations along the Niger River in an effort to re-establish traditional management institutions which existed in the region (Scudder and Conelly 1984; Sissoko et al. 1985). These traditional management institutions were disregarded by colonial governments that assumed responsibility for regulation of the river fisheries.

It seems inevitable that realization of OY will test our basic philosophies of renewable resource ownership and control. Do common property and open access rights preclude adequate protection of ecosystems and social benefits in most cases? If so, what are the most promising ways of allocating resource rights and allowing people to exercise control over riverine resources for maintenance of social values? What are the most efficient institutional combinations, local vs state vs federal, for meaningful cooperation and successful management plans? What are the modifications in institutional responsibilities that will help actualize OY?

Development Stage #5: Evaluation of Management

The final stage in the program development process shown in Fig. 1 is evaluation of system response to management action. Through evaluation, strong and weak aspects of management stategies will be identified so that modifications are possible. The process shown in Fig. 1 thus is cyclic, as evaluation of response to management leads to new, more refined, objectives. The development process thus becomes continuous and experimental, and reflects the adaptive management philosophy espoused by Walters (1986).

The specification of important system characteristics (Table 1) leading to data collection and analysis implies that system response to management can be evaluated by remeasuring the same set of descriptors subsequent to management action. Success can be judged by the magnitude of positive change in selected social descriptors. Evaluation should be an integral part of the management process — it is critical to purposeful evolution of fisheries science and will be required if we are to decide how best to address river management within the framework of optimum yield.

Conclusion

It is not necessarily the case that good sociological information will be used in a wise manner by those responsible for making decisions. True, there are formalized ways of integrating qualitative and quantitative data for decision-making purposes. Healey (1984) has used multiattribute analysis to formally address OY and there are applications of decision-making techniques to environmental and fisheries management problems in the literature (Bakus et al. 1982; Keeney 1982; Bain 1987). But, subjectivity is not removed from these analytical procedures because weighting coefficients must be derived for chosen attributes, most likely in an intuitive manner. Thus, although tools for structured decision-making may allow statistical processing of multiple attributes beyond the capabilities of the human organism, I don't know that the management alternatives favored by these analyses will be more socially equitable than those that might be chosen based on human decision-making, as intuitive as it might be. It is a strong reality, as Retting (1987) points out, that the use of "ordinary knowledge", i.e., knowledge based on common sense, casual empiricism, or thoughtful speculation and analysis, has been institutionalized into the policy process.

It must be recognized that there is no prescribed way, even within the comforts of our fisheries biology traditions, of integrating the various fish population and community descriptors that might be used for fishery assessment. We typically look at several characteristics of a fishery (some of which might be integrated in accordance with our population dynamics models, when applicable), hoping to find corroboration among some, so that we can be satisfied that the system is behaving in a particular way. Many times, sampling variability precludes meaningful statistical relationships, so that our final assessment of the situation is, more often than not, based on our best interpretation of the behavior of the variables, fully influenced by our particular personal experiences. If we can do no more than this with respect to using social account information for management and decision-making, then that is satisfactory for the time being. We must be patient and proceed with direction, keeping what works and discarding what does not. We must be socially accountable for our actions as natural resource managers and we must be serious about this responsibility. Only in this manner, will we gain the respect of the public that we serve, and at the same time, protect the health of our river ecosystems.

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References

BAILEY, C., C. K. HARRIS, AND C. K. VANDERPOOL. 1986. Future directions for fisheries sociology research, p. 125–130. *In* C. Bailey, C. Harris, C. Heaton, and R. Ladner [ed.] Proceedings of the Workshop of Fisheries Sociology. Woods Hole Oceanogr. Inst. Tech. Rep. WHOI-86-34: 124 p.

BAIN, M. B. 1987. Structured decision-making in fisheries management: trout fishing regulations on the Au Sable River, Michigan. North American J. Fish. Manage. 7: 475–481.

BAYLEY, P. B., AND M. PETRERE JR. 1989. Amazon fisheries: assessment methods, current status and management options, p. 385–398. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

BAKUS, J. B., W. G. STILLWELL, AND S. M. LATTER. 1982. Research decision making: with applications for environmental management. Environ. Manage. 6: 493–504.

BERKES, F. 1985. Fishermen and 'the tragedy of the commons'. Environ. Conserv. 12: 199–206.

BISHOP, R. C., K. J. BOYLE, AND M. P. WELSCH. 1987. Toward total economic evaluation of Great Lakes fishery resources. Trans. Am. Fish. Soc. 116 339–245.

CERNEA, M. M. 1984. Putting people first: the position of sociological knowledge in planned rural development. Sixth World Congress for Rural Sociology, International Rural Sociology Association, Manila.

DODGE, D. P. [ED.]. 1989. Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

GLASS, R. J., AND R. M. MUTH. 1987. Pitfalls and limitations in the use of fishery valuation techniques. Trans. Am. Fish. Soc. 116: 381–389.

HARDIN, G. 1968. The tragedy of the commons. Science 162: 1234–1246.

HARRIS, C. K. 1986. Toward a sociology of fisheries, p. 1–29. *In* C. Bailey, C. Harris, C. Heaton, and R. Ladner [ed.] Proceedings of the Workshop on Fisheries Sociology. Woods Hole Oceanogr. Inst. Tech. Rep. WHOI-86-34: 134 p.

HEALEY, M. C. 1984. Multiattribute analysis and the concept of optimum yield. Can. J. Fish. Aquat. Sci. 41: 1396–1406.

KEENEY, R. L. 1982. Decision analysis: an overview. Operations Res. 30: 803–838.

KERR, S. R. 1982. The role of external analysis in fisheries science. Trans. Am. Soc. 111: 165–170.

LUNVEN, P. 1983. The nutritional consequences of agricultural and rural development projects. Food Nutrition Bull. 4: 17–22.

MALVESTUTO, S. P. 1983. Sampling the recreational fishery, p. 397–419. *In* L. Nielsen and D. L. Johnson [ed.] Fisheries Techniques. American Fisheries Society, Bethesda, MD. 468 p.

MALVESTUTO, S. P., AND E. K. MEREDITH. 1989. Assessment of the Niger River fishery in Niger (1983-1985) with implications for management, p. 533-544. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

MARTIN, R. G. 1987. Economic impact analysis of a sport fishery on Lake Ontario: an appraisal of method. Trans. Am. Fish. Soc. 116: 461–468.

MATLOCK, G. C., G. E. SAUL, AND C. E. BRYAN. 1988. Importance of fish consumption to sport fishermen. Fisheries 13(1): 25–26.

NEWTON, N. 1983. Assessing nutritional status. Directions 3: 2–12.

PALM, R. C., AND S. P. MALVESTUTO. 1982. Relationships between economic benefit and sport fishing effort on West Point Reservoir, Alabama–Georgia. Trans. Am. Fish. Soc. 112: 71–78.

POLLNAC, R. B. 1985. Sociocultural issues in West African fisheries development. Anthropology Working Paper No. 45, International Center for Marine Resource Development, University of Rhode Island, RI. 26 p.

REGIER, H. A., AND A. P. GRIMA. 1985. Fishery resource allocation: an exploratory essay. Can. J. Fish. Aquat. Sci. 42: 845–859.

REGIER, H. A., R. L. WELCOMME, R. J. STEEDMAN, AND H. F. HENDERSON. 1989. Rehabilitation of degraded river ecosystems, p. 86–97. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

RETTIG, R. E. 1987. Bioeconomic models: do they really help fishery managers? Trans. Am. Fish. Soc. 116: 405–411.

SAVANE, M. A. 1982. Implications for women and their work: of introducing nutritional considerations into agricultural and rural development projects. Food and Nutrition Bulletin 3: 1–5.

SCUDDER, T., AND T. CONELLY. 1984. Management systems for riverine fisheries. Institute for Development Anthropology, Binghamton. NY. 87 p.

SEDELL, J. R., J. E. RICHEY, AND F. J. SWANSON. 1989. The river continuum concept: a basis for the expected ecosystem behavior of very large rivers?, p. 49–55. *In* D. P. Dodge [ed.]. Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

SHANER, W. W., P. F. PHILIPP, AND W. R. SCHMEHL. 1982. Farming systems research and development: guidelines for developing countries. Westview Press, Boulder, CO. 414 p.

SISSOKO, M. M., S. P. MALVESTUTO, G. M. SULLIVAN, AND E. K. MEREDITH. 1985. Inland fisheries in developing countries: an opportunity for a farming systems approach to research and management, p. 297–317. *In* C. B. Flora and M. Tomecek [ed.] Selected Proceedings of the Farming Systems Research Symposium, Kansas State University Office of International Agricultural Programs, Manhatten, KS. 548 p.

SMITH, C. L. 1983. Evaluating human factors, p. 431–445. *In* L. Nielsen and D. L. Johnson [ed.] Fisheries Techniques. American Fisheries Society, Bethesda, MD. 468 p.

TALHELM, D. R., AND L. W. LIBBY. 1987. In search of a total value assessment framework: SAFR symposium overview and synthesis. Trans. Am. Fish. Soc. 116: 293–301.

VANDERPOOL, C. K. 1986. Social impact assessment and fishery conservation and management, p. 49–62. *In* C. Bailey, C. Harris, C. Heaton and R. Ladner [ed.] Proceedings of the Workshop on Fisheries Sociology. Woods Hole Oceanogr. Inst. Tech. Rep. WHOI-86-34: 134 p.

WALTERS, C. 1986. Adaptive management of renewable resources. Macmillan Publishing Company, NY. 374 p.

Science Transfer Networks for Large River Management

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Abstract

BIETTE, R. M., G. A. GOODCHILD, AND S. J. NEPSZY. 1989. Science transfer networks for large river management, p. 600–606. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Traditional approaches used by resource management agencies to transfer science to the public have failed and consequently the public is unaware of the real issues in the management of large rivers. To improve this, an intragency network is described that conveys science directly to the public. As well, the tools that are needed for the establishment of a global network to facilitate international collaboration among large river workers are described. We suggest that both networks will result in management strategies required to protect and rehabilitate large rivers — the global network through the development of new science and the intragency network by involving the public and the activation of the political decision-making process.

Résumé

BIETTE, R. M., G. A. GOODCHILD, AND S. J. NEPSZY. 1989. Science transfer networks for large river management, p. 600–606. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Les approches traditionnelles de vulgarisation scientifique utilisées par les organismes de gestion des ressources ont été inefficaces de sorte que le public n'est pas conscient des véritables problèmes que pose la gestion des grands cours d'eau. Les auteurs décrivent un réseau interorganismes destiné à améliorer la situation en diffusant les données scientifiques directement au public. Ils décrivent aussi les instruments nécessaires à l'établissement d'un réseau international qui faciliterait la collaboration entre les gestionnaires des ressources des grands cours d'eau. Ils sont d'avis que les deux réseaux permettront de mettre sur pied des stratégies de gestion visant à protéger et à remettre en état les grands cours d'eau: le réseau international grâce au développement de nouvelles sciences et le réseau interorganismes grâce à la participation du public et à la stimulation de la prise de décisions politiques.

Introduction

Every river described at this symposium has been altered significantly by man (Dodge 1989). Large rivers have been dammed for power production and flood control; they have been channelized and dredged for navigation, and they have been used for disposal of wastes, including hazardous substances. Their fish communities have been further changed through overexploitation and the introduction of non-native species. As a result, most large rivers have become degraded and unable to support healthy fish assemblages. This degradation continues as new developments for further use and economic growth are planned. To reverse this trend, it is necessary to: (a) protect large rivers from further degradation and (b) reverse the effects of some of the damage as suggested by Regier et al. (1989). The achievement of this goal for large rivers requires some new strategies in their management. The purpose of this paper is to discuss two of these strategies developed through discussions by the LARS working group on the transfer of science relating to the status and management of large rivers.

Of foremost importance, there is a need to improve the way science is transferred from resource management agencies to the public. Because the value that the public places on natural resources, such as large rivers, is influenced by their knowledge, attitudes and beliefs about these resources (McDonough et al. 1987), it is essential to inform the public on the important issues facing large river management. More effective approaches, (see Loftus 1987) for transferring science to the public need to be developed for this purpose. Secondly, there is a need to build a global network to promote international collaboration among scientists, managers and institutions concerned with large rivers. The current state of knowledge of large river rehabilitation is limited because these complex systems are not well understood. Furthermore, there are relatively few persons engaged in large river research or management, and these people are scattered across the globe. A global network is needed to enable all persons engaged in large river work to communicate more effectively. Research scientists and managers could use this information-exchange network to collaborate on their endeavors and, in this way, develop the new science that is needed for large river rehabilitation.

This paper will examine some of the traditional methods that are used to transfer science, point out some of the insufficiencies of these methods, and then, using examples, propose an alternative and more effective approach for transferring science in agencies responsible for the management of large rivers. We will then discuss the tools that are required to build a global network to facilitate international collaboration among large river workers.

Traditional Approaches

The traditional approach of conveying science within most resource management agencies is illustrated in Fig. 1. Results of published research flow downward from the research scientist to the manager, who tries to apply it in managing the problems facing the resource. It then reaches the policymaker where it is transformed into policy and programs that are delivered to the public.

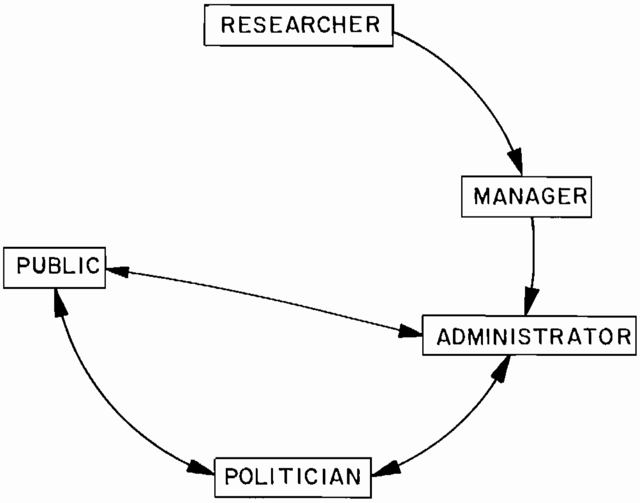

FIG. 1. Traditional approach to transfer science within resource management agencies.

There are several impediments to this method of science transfer. First, there are relatively few opportunities to deliver science to managers. Because research scientists strive for critical review from peers in response to publications, they publish their results in primary scientific journals and present their findings orally at scientific conferences. Consequently, most of the information is delivered to other research scientists. Because there is often inadequate synthesis and integration of the science into forms useful for management, the information that is conveyed to managers may not be of immediate use for management application. This situation limits the ability of managers to use science effectively and inhibits development of a long-term management perspective.

Secondly, in most agencies, there are limited opportunities for managers to describe their needs to scientists and there is inadequate guidance of scientific and technical activities by management. The absence of directions from managers as to priorities of research activities tends to limit the utility of research to management. The result is the familiar situation involving frustrated scientists who feel that managers are not listening or cannot understand, and managers who may choose to think that the kind of science being produced by scientists has no practical application. Ultimately, a breakdown of communication between research and management occurs.

Thirdly, in the traditional approach there is limited opportunity for the public to become well informed on long-term issues such as the protection and restoration of large rivers. In fact, there may be a barrier to the movement of useful information from the management organization to the public. Loftus (1987) pointed out that some management agencies have developed ''information branches'' which have become institutional constraints to the flow of useful information to the public. Such branches become dedicated to ''image building'' in support of political authority, thereby becoming less useful in providing support for resource management. The process is insidious and involves short-term cycles related to the time between elections which promotes quick turnaround projects and band-aid solutions that address symptoms rather than problems. Consequently, the resource cannot be effectively managed, let alone maintained or rehabilitated. Furthermore, when research scientists and managers have an opportunity to communicate with the public on specific issues, they often use scientific jargon which the public may not understand. As well, they may communicate in a style that is unfamiliar to a layperson and as a result, the scientist fails to inform adequately the public.

Finally, it takes too long (decades in the fisheries science field) for new information to become assimilated as science by managers and communicated to the public (Loftus 1984). This lag prohibits timely decisions on the management of large rivers.

Toward Better Science Transfer

To alleviate some of the problems in the transfer of science, some agencies and educators are developing new approaches. What follows are three case studies describing the science transfer efforts of the Tennessee Valley Authority, New York State and the Colorado State University to inform better the public on some of the issues pertaining to the Tennessee River, Hudson River and Colorado River, respectively.

Tennessee River: As with most agencies, the Tennessee Valley Authority (TVA) faces the continual challenge of translating highly specialized and complex science into information that the public can understand and use (C.W. Voigtlander pers. comm.). For instance, scientific findings must be distilled into information that concerned citizens groups could use when interacting with state and federal officials in the formulation of their positions on such diverse issues as reclamation of abandoned surface-mines, disposal of hazardous wastes, operation of reservoirs, and development of hydro power and land.

Early attempts involving annual conferences with these public interest groups revealed two important factors:

1) Communication must involve the scientific and technical staff of the TVA rather than the public information officers. The latter are viewed as public relations staff at best and as agency apologists at worst.
2) Communication is not effective if all of the initiative in defining and discussing a given issue remains solely or is perceived to remain with the agency. Such efforts are seen as "dog-and-pony shows" designed to justify ongoing or proposed agency programs and projects.

To improve this situation, an informal communication process was initiated to allow the citizens' organizations to identify issues of interest. These organizations then produced position papers which were circulated to all interested organizations and to the Environmental Quality Staff of the TVA. The Environmental Quality Staff then organized the annual conference. The scientific staff review and respond to the position papers, attend the conference, and identify other agency staff necessary for conference participation. This approach is somewhat analogous to the one used by the North American Lake Management Society to facilitate the exchange of information with the public (NALMS 1987).

While not all controversies are resolved through this process, the following positive effects have been noted:

1) Scientific staff have the opportunity to present and explain their data.
2) Citizen interest groups have the opportunity to make known their views, and to obtain additional information which may reinforce or modify their views. In either case, their position is strengthened when dealing with decision-makers and legislators.
3) The TVA is able to determine and clarify the issues that are important to the public and can use this information in planning management programs and making decisions on resource development.

Hudson River: During the 1960s, the Hudson was considered "dead", unaesthetic, and a dumping ground for sanitary and industrial waste. Recently, there has been a change in public attitude toward the Hudson River. The Hudson River is being seen more as a scenic and recreational resource. Apartments and buildings with views of the Hudson are at a premium, fishing tournaments are flourishing and companies which offer tours of the lower Hudson are increasing. In addition, there is increasing coverage on the river by local and national media, and scientists are turning their attention to research issues associated with the Hudson River (Limburg et al. 1989).

Concurrent with this change in attitude, major efforts have been made to provide the public with information about the Hudson River environment (J.C. Cooper pers. comm.). Firstly, the Hudson River Foundation for Science and Environmental Research was established in 1981 under the terms of a settlement agreement among environmental groups, government regulatory agencies and utility companies seeking the solution of a long series of legal battles over the environmental impact of power plants on the Hudson River. The Foundation supports research, education and environmental improvement programs concerning all aspects of the Hudson River ecosystem. For example, by the end of 1986, more than 100 grants and contracts, totalling $3.4 million were awarded. In addition to supporting research, the Fund also sponsors workshops and conferences, bringing together authorities working within the Hudson River valley to discuss relevant scientific or public policy issues. For instance, each year the Foundation sponsors a Hudson River Symposium to improve public understanding and appreciation of the Hudson River ecosystem. At this gathering, the public hears presentations by scientists on their work, and scientists are asked to present and discuss their work in a format that will be understandable by the public. Use of unexplained technical terms and jargon are discouraged. As a result, there has been a significant improvement in communication at this symposium since its beginning three years ago.

Secondly, legislation was passed to create a Hudson River Fisheries Advisory Committee. This committee of State scientists, managers, fishermen and interested laypersons meets regularly to discuss issues of importance to fisheries. In 1984, a Hudson River Coordinator was appointed. The Coordinator chairs the advisory committee and acts as a liaison between the state and local interest groups. Thirdly, a privately funded riverkeeper position was established to act as a roving ombudsman to bring to the attention of both the public and management any activities that may degrade the river. The success of these arrangements is dependent on the willingness of the State to act as a clearinghouse for information to the public. As well, public interest groups must continue to be aware of the current research and be willing to become better informed on the issues. Scientists, on the other hand, must learn to be broader in their approaches and willing to devote at least a modicum of their time to public education.

Colorado River: Several approaches have been employed in the past to promote public awareness of the Colorado River and its unique biota. Fishery managers and scientists have described the river's altered condition (Carlson and Muth 1989) through scientific and technical papers, non-technical articles published by university extension services and fishery resource agencies, and presentations at public meetings and schools. Additionally, the Colorado Division of Wildlife sponsors an education program called "Project Wild" designed to interest high school students in wildlife conservation. Despite these efforts, public attitudes toward values of rare fishes of the Colorado River remain somewhat negative. This attitude was the case in northwestern Colorado when a proposal for a new dam on a major tributary of the Colorado River was reviewed recently. Newspapers featured articles on the "wasted" efforts of fisheries biologists in trying to protect rare and endangered fish species in the river, and some articles stated that the rare species were common, and not endangered at all. At the same time, water conservation districts were promoting plans to build additional dams for agricultural and economic development. Further, incidents of deliberate killing of endangered fishes were documented in the area.

To enhance public awareness of the trade-offs inherent in construction of additional dams on the Colorado River, scientists at Colorado State University have proposed a more intensive grass-roots public education program for northwestern Colorado (C.A. Carlson pers. comm.). The objectives of this program are to (1) inform better the public on the issues and, (2) encourage the public to make their opinions known to decision-makers. Educational packages will be developed for presentation at schools and public meetings. The program is to foster willingness to live harmoniously with, rather than dominate, nature. Appreciation for unique life forms, as expressed by Wilson (1984), Rolston (1985), and Callicot (1986), are to be emphasized. Researchers proposed to concentrate efforts on the young, who have fewer preconceived notions than their elders and may, in time, be able to influence them favourably. Funding for this program is presently being explored.

Conceptual Framework: On the basis of these case studies and from our own experiences, we propose a conceptual framework for improving science transfer within resource management agencies (Fig. 2). In this framework, science is conveyed from the research scientist to the public. Further, the pathway from the research scientist to the manager is strengthened so that science is delivered directly to the managers and not just through scientific reports and conferences. In addition, a pathway is provided for the manager to convey the assimilated science to the public. Thus, unlike the traditional approach, science is conveyed to the public by both research scientists and managers and not just by public relations staff or administrators. Consequently, the public should develop an improved understanding and appreciation of the river ecosystem and the issues that affect it. The public can then use this knowledge when it interacts with the politicians and decision-makers and this could result in support for the kinds of political decisions that are needed to protect and restore large rivers. Also, because science is delivered directly to the manager and the public, the time required for new information to become assimilated is reduced.

There are also some important feedback links in this scheme that are absent in the traditional approach. There is a feedback link between the public and manager and one between the public and researcher. These links allow the public to express their views, influence both research and management priorities, and participate in management activities. There is also a feedback link between manager and reseacher so that the manager can influence more effectively research priorities, and the one between administrator and manager is strengthened so that more appropriate management programs can be implemented. These feedback links enable both the public and various levels in the hierarchy of the resource agency to develop the expertise for making scientifically sound judgments about the use of a river's resources.

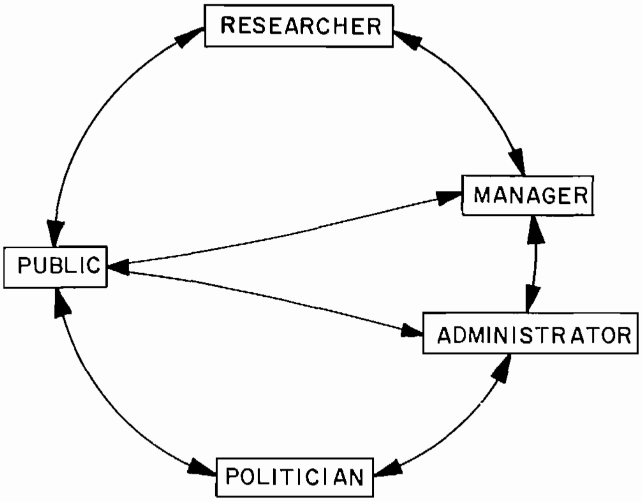

FIG. 2. A conceptual framework for improving science transfer within resource management agencies.

In order to illustrate how this conceptualized scheme could be applied by a resource management agency, we have incorporated in Fig. 3 the science transfer components into the generalized planning process of resource agencies described by Crowe (1983). For instance, a resource management agency would first determine the present status of its science transfer programs. The inventory might include items such as the number of scientific publications written by staff, the number of scientific conferences attended, the number of news releases written for the press, or the cost of providing information to the public. Two of these items are illustrated on Fig. 3. The next step would be to develop some strategies to improve science transfer within the agency. The strategies might be to better inform the public on management issues and to develop a more efficient science transfer program (Fig. 3). An operational plan would then be developed. For example, the agency may want to develop an educational package for the school program, establish a Citizen Advisory Council to assist in communicating with the public, hold a series of workshops to transfer science to management or train staff in communicating with the public. To complete the cycle, the agency would have to develop mechanisms to evaluate the progress of these plans. In Fig. 3, two examples are illustrated: (1) to monitor changes in the public's attitude towards a particular resource and (2) to monitor the number of educational packages used in schools.

Several implications result from this approach. Scientists and managers will need training in public speaking and media presentation. They will need to become familiar with the techniques of the public communication process, such as stating the message clearly, knowing the audience so that the message is expressed from the viewpoint of the public's interest and stating the main point of the message at the beginning. Workshops, public meetings and information papers will be needed for the exchange of information with the public. River coordinators or river advisory councils will need to be established to act as contact persons for the public. Opportunities for the public to participate in the management process may also be needed. For example, public involvement programs or other partnership arrangements with the public may need to be explored. Education programs are needed at all age levels to increase the level of understanding of the public on the complex issues associated with rivers. Such programs will involve the preparation of educational kits, as well as integrating this material into the school system. Structured opportunities, such as workshops, will be needed for scientists to deliver science to managers. The science will have to be synthesized and integrated into a usable form for management. As well, opportunities for managers to describe their needs to scientists and thus influence scientific priorities will have to be established. All of these activities will require planning, time and resources. Agencies' budgets will need to reflect these changes in priorities.

Global Network

The second initiative that is needed to achieve the goal of protecting and restoring large rivers is to develop a global network for the facilitation of collaboration among large

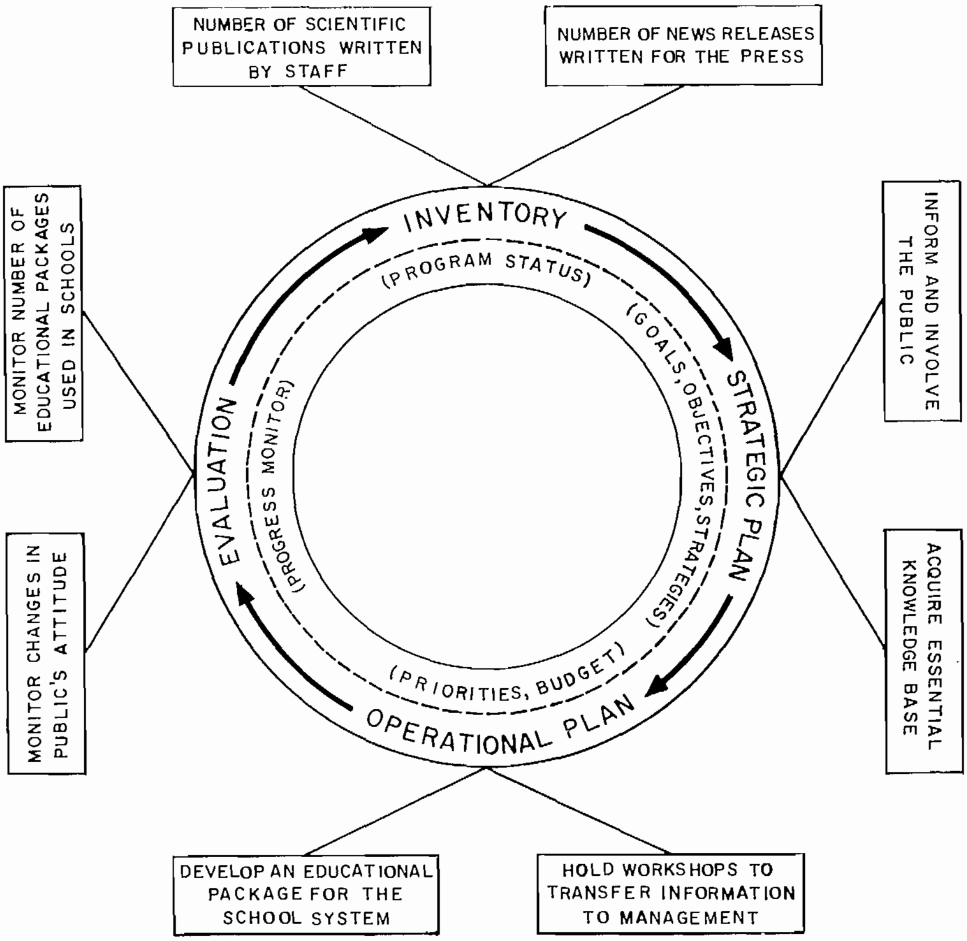

FIG. 3. The science transfer components incorporated into the planning process of resource management agencies. Adapted from Crowe (1983).

river workers. This collaboration is essential because of the complex nature of large rivers, the limited understanding of them and the limited human and monetary resources available for the study of these systems. It is only through the sharing of information and pooling of these resources that it will be possible to acquire the necessary new knowledge needed to better manage large rivers. The global network would provide the persons engaged in large river research and management access to the information that they need for the development of this new science.

This needed collaboration among river workers was initiated at LARS. The interchange at LARS provided information on the status and management of 33 large rivers across the globe. Comparisons and contrasts between rivers of the world were made. Information known about other ecosystems was pooled with that on large rivers (e.g. Ryder and Pesendorfer 1989; Sedell et al. 1989; among others). In addition, there was a sharing of information from many disciplines (e.g. Kellerhals and Church 1989; Ellis and Woitowich 1989, and Stalnaker et al. 1989; among others). This type of exchange is essential for creating the new knowledge base needed to manage large rivers. Furthermore, a network for collaboration among large river workers in Europe has been established recently by the Council of Europe (A.L. Roux pers. comm.). This network addresses water management in the alluvial valleys of large rivers and is part of the European network of scientific and technical cooperation. The proposed global network would build on this exchange and continue with the momentum generated at LARS. The following tools are recommended to develop this global network:

1) Hold a follow-up symposium to LARS in five years time. This symposium would provide an opportunity to (a) reexamine some of the reported case histories presented at LARS with regard to the status of the major stresses and their effects on the fish communities and other bellwethers of the health of the ecosystem, and (b) evaluate a trend-through-time assessment of some of the key parameters (nutrients, hydraulics, standing stocks, etc.) that are needed for better management. The symposium could be held in conjunction with an ongoing series of International Symposia concerned with research on regulated rivers. Four Symposia have been held: in Erie, USA (1979), Oslo, Norway (1982), Edmonton, Canada (1985) and Loughborough, England (1988). These Symposia attracted scientists, academics and engineers from many countries and from every continent. The aim of the Series is to foster an exchange of ideas and to stimulate research (G.E. Petts pers. comm.).
2) Establish a newsletter on large river management. A newsletter would maintain a dialogue between LARS

participants and other interested people, provide information on where people are located and what they are working on, as well as reporting on upcoming events and other sources of information. The newsletter could be developed as an extension from the Large European Alluvial Rivers Newsletter, referred to as LEARN (A.L. Roux pers. comm.). Since Fall, 1986, LEARN has been published semi-annually for the coordinators and members of the European large river network.

3) Establish a directory of persons engaged in large river research and management. This directory would become a 'who's who' in large river work and would document the persons' organization, expertise, special interests, etc. The directory could be modelled after the American Fisheries Society's ''Directory of Fisheries Scientists'' (AFS 1988). It would need to be updated periodically.
4) Establish a collection of reference material on large rivers. A small collection of several hundred references with a bibliography was developed for LARS. This material could form the basis for developing a LARS library. An accessible research or management agency could take custody of this material, update it regularly and make it available for the use of all persons engaged in large river work across the globe.
5) Prepare training and educational material on large rivers. The LARS library and LARS proceedings should be made available to educators around the world and used as a basis for preparing appropriate educational material. Perhaps, the approach taken for the Colorado River, described above, could serve as a model for this task and be used to assist others. In any case, various agencies should learn from the experiences of others and assist each other as much as possible. For example, photographs, brochures, posters, video tapes and other visual aids could be shared among educators. In addition, the proceedings should be used by management agencies for training at workshops on large river management.
6) Develop an exchange program for researchers, managers and students studying large rivers. This exchange would facilitate the sharing of science on large rivers as well as help build an international collaboration for large river management and research. Exchanges of scientists from various continents have been used successfully for both ocean and lake research work, but few have occurred for large rivers.
7) Make better use of some of the existing vehicles that are established for international communications. For instance, promote the publishing of scientific findings and management activities on river systems in international journals so that the information is more readily available. For example, publish in the journal Regulated Rivers, Research and Management. This is an international journal dedicated to the promotion of interdisciplinary research concerned with river management (Petts 1987). Make use of existing electronic bulletin boards, such as the one developed by the American Fisheries Society, to communicate with other workers. Maintain close liaison with national and international agencies and encourage worldwide support of large river studies through FAO programs, United Nations Environmental Programs (UNEP) and the International Union for the Conservation of Nature (IUCN), among others. To attract worldwide attention to large rivers, Davies and Walker (1986) made an appeal to establish a global Year of the River System. They point out that this would complement other international campaigns promoting trees (1984), wetlands (1985) and islands (1986). This attention would not only promote public awareness, but also encourage international collaboration.

In conclusion, developing a global network for international collaboration will help to increase the understanding of large rivers. In turn, this information will be conveyed through the science transfer system within agencies to make the public aware of the issues and thus be the basis for generating the political will necessary to support long-term strategies for riverine rehabilitation.

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References

AMERICAN FISHERIES SOCIETY. 1988. 1987 Membership Directory and Handbook. Bethesda, MD. 106 p.

CALLICOTT, J. B. 1986. On the intrinsic value of non-human species. p. 138–172. *In* B. G. Norton [ed.] The preservation of species: the value of biological diversity. Princeton University Press, Princeton, NJ.

CARLSON, C. A., AND R. T. MUTH. 1989. The Colorado River; lifeline of the American Southwest, p. 220-239. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

CROWE, D. M. 1983. Comprehensive planning for wildlife resources. Wyoming Game and Fish Dep. WY. 143 p.

DAVIES, B. R., AND K. F. WALKER. 1986. The ecology of river system. Dr. W. Junk Publishers, Dordrecht. 793 p.

DODGE, D. P. [ed.] 1989. Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

ELLIS, J. T., AND W. A. WOITOWICH. 1989. An overview of the use of remote sensing for the study of rivers and river systems, p. 98–109. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

KELLERHALS, R., AND M. CHURCH. 1989. The morphology of large rivers: characterization and management, p. 31–48. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

LIMBURG, K. E., S. A. LEVIN, AND R. E. BRANDT. 1989. Perspectives on management of the Hudson River ecosystem, p. 265–291. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium Can. Spec. Publ. Fish. Aquat. Sci. 106.

LOFTUS, K.H. 1984. Fisheries: past, present and future in the Great Lakes. J. Great Lakes Res. 10: 164–167.

1987. Inadequate science transfer: an issue basic to effective fisheries management. Trans. Am. Fish. Soc. 116: 314–319.

MCDONOUGH, M. H., M. COBB, AND D. F. HOLECEK. 1987. Role of communication science in social valuation of fisheries. Trans. Am. Fish. Soc. 116: 519–524.

NORTH AMERICAN LAKE MANAGEMENT SOCIETY. 1987. Annual Report. Washington, DC. 21 p.

PETTS, G. E. [Editor-in-Chief]. 1987. Aims and scope, regulated rivers: research and management. 1: 95.

REGIER, H. A., R. L. WELCOMME, R. J. STEEDMAN, AND H. F. HENDERSON. 1989. Rehabilitation of degraded river ecosystems, p. 86–97. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

ROLSTON, H. 1985. Duties to endangered species. BioScience 35: 718–726.

RYDER, R. A., AND J. PESENDORFER. 1989. Large rivers are more than flowing lakes: a comparative review, p. 65–85. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

SEDELL, J.R., J. E. RICHEY, AND F. J. SWANSON. 1989. The river continuum concept: A basis for the expected ecosystem behaviour of very large rivers, p. 49–55. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

STALNAKER, C. B., R. T. MILHOUS, AND K.D. BOVEE. 1989. Hydrology and hydraulics applied to fishery management in large rivers, p. 13–30. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

WILSON, E. O. 1984. Biophilia. Harvard University Press, Cambridge, MA.

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LARS Epilogue

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In 1971, the Salmonid Community in Oligotrophic Lakes (SCOL) Symposium, a first of its kind, set the stage for other innovative symposia sponsored by the Province of Ontario (Loftus and Regier 1972). The International Large River Symposium (LARS) followed the SCOL tradition in the sense that it has generated more questions pertaining to river ecology than was possible for it to answer on the basis of available knowledge. Nonetheless, substantial progress was made with some of the most vexing river ecology problems shared by scientists and managers the world over. By providing a forum for information exchange, LARS not only raised the level of awareness of the important ecological role played by rivers within the global ecosystem, LARS also identified fishes specifically as ecologically important and economically valuable products of rivers. Unfortunately, relatively few long-term data sets exist of quantitative sufficiency to be useful for the prediction of fish yields from large rivers.

However, an heuristic model proposed by Welcomme et al. (1989) during the LARS discourse, may now be usefully applied for the purpose of gaining rapid conceptual insight into the problem of fish yield estimation in large rivers. Such an approach will assist river basin managers in making timely, first approximation yield estimates. This advancement alone does not preclude the need for long-term data series derived from well conceived monitoring programs. Only through the implementation of sustained assessment will precise yield estimates be achieved in the future.

Within North America, fisheries administrators have traditionally placed greater emphasis on research and management for lentic rather than lotic systems. This somewhat biased treatment of aquatic ecosystems has produced comprehensive, orderly data collections over time for lakes, but only sporadic, inconsistent data sets for rivers. This dichotomy is not easily rectified without conscious effort directed towards systematic data collections for lotic systems. Complementing this approach is the opportunity for information transfer between scientists working in lentic and lotic systems. However, this may be accomplished effectively only with a comprehensive understanding of the similarities and differences that exist between the two aquatic systems (Ryder and Pesendorfer 1989). LARS recognized large rivers as singularities, that is, unique ecological entities closely tied to their riparian environs, and therefore affected by both natural and anthropogenic events within their catchments. Rivers are characterized by distinct structural formations such as the hyporheic zone, and have unusual patterns of nutrient transport (spiralling) or biota distribution (drift). The River Continuum Concept (RCC) attempted to subsume these various phenomena under a generalized model that would have global application. In this it was largely successful (Vannote et al. 1980). However, information presented at LARS demonstrated that there were many variations on the RCC theme, yet none so disparate as to destroy confidence in the original concept. As an example, the work of Junk et al. (1989), demonstrated that downstream nutrient spiralling is an ineffective mode of nutrient transport in large tropical rivers such as the Amazon. There, lateral movements of nutrients from the floodplains to the mainstem channel constituted the principal mode of nutrient transport. Such seeming exceptions to "global rules" for ecosystem structure or behaviour need not require abandonment of the rule, but rather a reasoned accommodation of the rule to the exception. Of such considered accommodations is scientific progress made.

One aspect of major concern to LARS participants was the lack of technological development of appropriate gears and methodologies for the sampling of flowing waters and their biota. If useful quantitative measurements are to be made of lotic systems and all the biota contained therein, then effective gears and methodologies must be developed to address that need. Large, deep rivers, with high water velocities, are particularly intractable in this regard (Dr J. M. Casselman, Ontario Ministry of Natural Resources, Lake Ontario Fisheries Unit, RR #4, Picton, Ont. K0K 2T0, personal communication). In the future, emphasis should be placed on specialized technology designed for application to large rivers, particularly for the purpose of monitoring fish communities and their associated habitats. Significant progress could be effected expeditiously through redesign of vessels and gear used originally for the study of lakes or oceans (Hynes 1989).

One of the predominant themes that continually emerged throughout the duration of the LARS discourse was the extent of man's deleterious influence on large river basins (e.g. Ebel et al. 1989). Large rivers attract development, support shipping and other commercial ventures and are vulnerable to all of man's many environmental insults. Most of man's activities within a catchment such as agriculture and forestry, even when remote from the main drainage channel, ultimately wreak havoc on the mainstem. This effect is virtually universal in large river systems of developed countries in the north-temperate climatic zone such that the river mainstem itself serves as a useful indicator of watershed abuse. Extensive degradation emanating from demophoric effects are usually less threatening in developing countries. These circumstances are not encouraging however, as they represent only less intensive settlement or sparse levels of industrial development within catchments, rather than lessons learned from the experiences of developed countries and successfully applied by judicious third world governments.

There are major difficulties to be overcome if rehabilitation of degraded rivers and their fish communities are ever to become a reality. Because of the multiple uses of rivers for conflicting purposes, any plan for rehabilitation must be a broad-based approach that considers the degradation level not only of the river proper, but also of its catchment and tributaries, including the effects of atmospheric fallout. Under these circumstances, only an holistic, integrated and interdisciplinary ecosystem approach to rehabilitation and management may be reasonably acceptable. Rehabilitation is a recognized remedial philosophy for the restoration of large rivers to their natural state. However, it poses a two-pronged dilemma for ecosystem managers. First is the need to recognize the desired state and second is the need to anticipate the consequences of the rehabilitation measures that will be taken (e.g. Christie et al. 1987). Finally, the system must be managed effectively before, during and after the rehabilitation initiative. Accordingly, as in the case of fisheries that are exposed to an ever changing milieu, different management schemes must be developed over the course of the rehabilitation process. In virtually all instances of successful rehabilitation of large rivers, it is essential to retain or re-establish some semblance of the natural hydrological cycle (Junk et al. 1989).

Successful management of large rivers requires not only an ecosystemic outlook but also mechanisms to promote the efficient transfer of the apposite science (Biette et al. 1989). Science transfer occurs at several different nodes within our current institutional arrangements. To be effective, river science that is generated by researchers from government, universities or the private sector, should be first directed to "hands-on" managers as well as to senior resource administrators. Following suitable transformation, river science may also be provided to politicians with responsibilities for resource or environmental management and also to public user groups who influence these same politicians.

Many of the problems associated with river management stem from the differing policies and attitudes of contiguous jurisdictions that share a catchment. Government policies advocating massive industrialization of river valleys may be redirected following broad-based analyses by an interdisciplinary management team supported by an informed public. In these instances, derived long-term benefits will supercede short-term interests or profits (Kerrio 1989). Where jurisdictions are unable to agree on appropriate long-term management policies for a shared river basin, new formal agreements or institutions may generate the appropriate vehicle for a non-partisan approach to management policies. In any event, political will lacking public support invariably fails, thereby underlining the need for governments to commit resources that will adequately inform and involve the public in river management programs.

A need exists for the future fulfillment of many of the initiatives undertaken by LARS. Of foremost concern here is the establishment of an information network among scientists working within many disciplines dealing with river ecology. Preparation of compendia, syntheses and bibliographies relating to any aspect of river ecology should be cooperatively undertaken and made available to interested scientists. Currently, the existence of inexpensive computer bulletin boards, accessible essentially from anywhere on the face of the globe, makes information of this genre readily available through down-loading. Shorter documents may be facsimileed in a matter of seconds, from one phone terminal to virtually any other phone terminal in the world.

Other networking initiatives among scientists may be accomplished through interactive workshops addressing common problems such as toxic contaminants or shared rivers crossing several jurisdictions such as the Rhine (Lelek 1989) or the Mississippi (Fremling et al. 1989).

Foremost among future LARS options should be the consideration of another interdisciplinary, large river symposium to evaluate the progress made in the deficient areas highlighted by the LARS symposium in 1986. In addition, the next symposium should attempt to consolidate further both the science and the management policies that emanated from the LARS symposium, and to address new concepts or concerns that have arisen in the intervening years. LARS has made great and meaningful inroads into the consolidation of appropriate science for the future wise management of our large rivers. The challenge now is to maintain the momentum.

References

BIETTE, R. M., G. A. GOODCHILD, AND S. J. NEPSZY. 1989. Science transfer networks for large river management, p. 600–606. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

CHRISTIE, W. J., AND G. R. SPANGLER. 1987. International Symposium on Stocks Assessment and Yield Prediction. Can. J. Fish. Aquat. Sci. 44 (Suppl. 2): 1–501.

EBEL, W. J., C. D. BECKER, J. W. MULLAN, AND H. L. RAYMOND. 1989. The Columbia River — toward a holistic understanding, p. 205–219. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

FREMLING, C. R., J. L. RASMUSSEN, R. E. SPARKS, S. P. COBB, C. F. BRYAN, AND T. O. CLAFLIN. 1989. Mississippi River fisheries: a case history, p. 309-351. *In* D.P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

HYNES, H. B. N. 1989. Keynote address, p. 5–10. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

JUNK, W. J., P. B. BAYLEY, AND R. E. SPARKS. 1989. The flood pulse concept in river–floodplain systems, p. 110–127. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

KERRIO, V. G. 1989. A political view of large river management, p. 11–12. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

LELEK, A. 1989. The Rhine River and some of its tributaries under human impact in the last two centuries, p. 469–487. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

LOFTUS, K. H., AND H. A. REGIER. 1972. Introduction to the Proceedings of the 1971 Symposium on Salmonid Communities in Oligotrophic Lakes. J. Fish. Res. Board Can. 29: 617–628.

RYDER, R. A., AND J. PESENDORFER. 1989. Large rivers are more than flowing lakes: a comparative review, p. 65–85. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Can. J. Fish Aquat. Sci. 37: 130–137.

Welcomme, R. L., R. A. Ryder, and J. A. Sedell. 1989. Dynamics of fish assemblages in river systems — a synthesis, p. 569–577. *In* D. P. Dodge [ed.] Proceedings of the International Large River Symposium. Can. Spec. Publ. Fish. Aquat. Sci. 106.

Appendix

All LARS manuscripts were reviewed to confirm taxonomically acceptable scientific and common names of fish species. From this, a phylogenetic master list of fish species and their occurrence by river was compiled.

North America Arctic Rivers and Hudson Bay Drainage	Mackenzie and Churchill (Bodaly et al. 1989)	Moose River Basin (Brousseau and Goodchild 1989)	Northern Quebec R. (Roy 1989)
PETROMYZONTIDAE	X		
ACIPENSERIDAE			
Acipenser fulvescens	X	X	X
HIODONTIDAE			
Hiodon alosoides	X	X	X
Hiodon tergisus		X	X
SALMONIDAE			
Coregonus artedii	X	X	X
Coregonus autumnalis	X		
Coregonus clupeaformis	X	X	X
Coregonus nasus	X		
Coregonus sardinella	X		
Prosopium cylindraceum			X
Salmo gairdneri	X	X	
Salmo salar			X
Salvelinus alpinus	X		X
Salvelinus fontinalis	X	X	X
S. fontinalis timagamiensis		X	
S. fontinalis × *S. namaycush*		X	
Salvelinus namaycush	X	X	X
Stenodus leucichthys	X		
Thymallus arcticus	X		
OSMERIDAE	X		
ESOCIDAE			
Esox lucius	X	X	X
CYPRINIDAE	X		
Couesius plumbeus		X	X
Notemigonus crysoleucas		X	
Notropis atherinoides		X	X
Notropis cornutus		X	
Notropis hererolepis		X	
Notropis hudsonius		X	X
Phoxinus eos		X	
Phoxinus neogaeus		X	
Pimephales promelas		X	
Rhinichthys cataractae		X	X
Semotilus atromaculatus			X
Semotilus corporalis		X	X
Semotilus margarita		X	X
CATOSTOMIDAE			
Catostomus catostomus	X	X	X
Catostomus commersoni		X	X
Moxostoma sp.		X	
ICTALURIDAE			
Ictalurus nebulosus		X	
PERCOPSIDAE	X		
Percopsis omiscomaycus		X	
GADIDAE			
Lota lota	X	X	X
GASTEROSTEIDAE	X		
Gasterosteus aculeatus		X	X
Culaea inconstans		X	X
Pungitius pungitius		X	X
CENTRARCHIDAE			
Ambloplites rupestris		X	
Lepomis gibbosus		X	
Micropterus dolomieui		X	
PERCIDAE			
Etheostoma exile		X	
Etheostoma nigrum		X	
Perca flavescens		X	X
Percina caprodes		X	X
Stizostedion canadense		X	X
Stizostedion vitreum	X	X	X
SCIAENIDAE			
Aplodinotus grunniens		X	
COTTIDAE	X		
Cottus bairdi		X	X
Cottus cognatus		X	X
Cottus ricei			X

North America Pacific Drainage Rivers	Fraser (Northcote and Larkin 1989)	Columbia (Ebel et al. 1989)	Colorado (Carlson and Muth 1989)
PETROMYZONTIDAE			
Lampetra ayresi	X		
Lampetra richardsoni	X		
Lampetra tridentata	X		
ACIPENSERIDAE			
Acipenser medirostris	X		
Acipenser transmontanus	X	X	
ELOPIDAE			
Elops affinis			X
CLUPEIDAE			
Alosa sapidissima	X	X	
Clupea harengus	X		X
Dorosoma petense			X
SALMONIDAE			
Coregonus clupeaformis	X		
Oncorhynchus gorbuscha	X		
Oncorhynchus keta	X		
Oncorhynchus kisutch	X	X	X
Oncorhynchus nerka	X	X	X
Oncorhynchus tshawytscha	X	X	
Prosopium coulteri	X		
Prosopium williamsoni	X	X	X
Salmo apache			X
Salmo clarki	X	X	X
Salmo gairdneri	X	X	X
Salmo gilae			X
Salvelinus confluentus	X		
Salvelinus fontinalis	X		X
Salvelinus malma	X		
Salvelinus namaycush	X		
OSMERIDAE			
Hypomesus pretiosus	X		
Spirinchus thaleighthys	X		
Thaleichthys pacificus	X	X	
ESOCIDAE			
Esox lucius			X
CYPRINIDAE			
Acrocheilus alutaceus	X		
Agosia chrysogaster			X
Carassius auratus	X		
Couesius plumbeus	X		
Cyprinus carpio	X		
Gila cypha			X
Gila elegans			X
Gila intermedia?			X
Gila robusta			X
Hybognathus hankinsoni	X		
Lepidomeda albivallis			X
Lepidomeda altivelis			X
Lepidomeda mollispinis			X
Lepidomeda vittata			X
Meda fulgida			X
Moapa coriacea			X
Mylocheilus caurinus	X		
Plagopterus argentissimus			X
Ptychocheilus lucius			X
Ptychocheilus oregonensis	X	X	
Rhinichthys cataractae	X		
Rhinichthys deaconi?			X
Rhinichthys falcatus	X		
Rhinichthys osculus			X
Richardsonius balteatus	X		X
Tiaroga cobitis			X
CATOSTOMIDAE			
Catostomus catostomus	X		
Catostomus clarki			X
Catostomus columbianus	X		
Catostomus commersoni	X		
Catostomus insignis			X
Catostomus latipinnis			X
Catostomus macrocheilus	X		
Catostomus platyrhynchus	X		X
Xyrauchen texanus			X
ICTALURIDAE			
Ictalurus nebulosus	X		
Ictalurus punctatus			X
Pylodictis olivaris			X
GADIDAE			
Lota lota	X		
Microgadus tomcod	X		
CYPRINODONTIDAE			
Cyprinodon macularius			X
Crenichthys baileyi			X
Crenichthys nevadae			X
POECILIIDAE			
Gambusia affinis			X
Poecilia latipinna			X

North America Pacific Drainage Rivers	Fraser (Northcote and Larkin 1989)	Columbia (Ebel et al. 1989)	Colorado (Carlson and Muth 1989)
Poeciliopsis occidentalis			X
GASTEROSTEIDAE			
Gasterosteus aculeatus	X		
PERCICHTHYIDAE			
Morone saxatilis			X
CENTRARCHIDAE			
Lepomis gibbosus	X		
Micropterus dolomieui		X	
Micropterus salmoides		X	
Pomoxis nigromaculatus	X		
Pomoxis spp.		X	
PERCIDAE			
Perca flavescens		X	
Stizostedion vitreum		X	
CICHLIDAE			
Tilapia zilli			X
MUGILIDAE			
Mugil cephalus			X
ELEOTRIDAE			
Eleotris picta			X
COTTIDAE			
Cottus aleuticus	X		
Cottus asper	X		
Cottus bairdi			X
Cottus beldingi			X
Cottus cognatus	X		
Cottus rhotheus	X		
Leptocottus armatus	X		
Synchirus gilli	X		
EMBIOTOCIDAE			
Cymatogaster aggregata	X		
PLEURONECTIDAE			
Platichthys stellatus	X		

North America Atlantic Drainage rivers	Laurentian Great Lakes (Edwards et al. 1989)	Hudson (Limburg et al. 1989)	Miramichi (Randall et al. 1989)
PETROMYZONTIDAE			
Ichthyomyzon unicuspis		X	
Lampetra appendix		X	
Petromyzon marinus		X	
ACIPENSERIDAE			
Acipenser brevirostrum		X	
Acipenser fulvescens	X		
Acipenser oxyrhynchus		X	X
LEPISOSTEIDAE			
Lepisosteus osseus	X		
AMIIDAE			
Amia calva		X	
ANGUILLIDAE			
Anguilla rostrata		X	X
CLUPEIDAE			
Alosa aestivalis		X	X
Alosa pseudoharengus	X	X	X
Alosa sapidissima		X	X
Brevoortia tyrannus		X	
Dorosoma cepedianum	X	X	
HIODONTIDAE			
Hiodon tergisus	X		
SALMONIDAE			
Coregonus artedii	X	X	
Coregonus clupeaformis	X	X	
Prosopium cylindraceum		X	
Oncorhynchus gorbuscha	X		
Oncorhynchus kisutch	X		
Oncorhynchus nerka		X	
Oncorhynchus tshawytscha	X		
Prosopium cylindraceum	X		
Salmo salar		X	X
Salmo gairdneri	X	X	
Salmo trutta		X	
Salvelinus alpinus			X
Salvelinus fontinalis	X	X	X
Salvelinus namaycush	X	X	
OSMERIDAE			
Osmerus mordax	X	X	X
UMBRIDAE			
Umbra limi		X	
Umbra pygmaea		X	

North America Atlantic Drainage rivers	Laurentian Great Lakes (Edwards et al. 1989)	Hudson (Limburg et al. 1989)	Miramichi (Randall et al. 1989)
ESOCIDAE			
Esox americanus		X	
Esox lucius	X	X	
Esox masquinongy	X		
Esox niger		X	
CYPRINIDAE			
Carassius auratus	X	X	
Clinostomus elongatus		X	
Couesius plumbeus		X	X
Cyprinus carpio	X	X	
Exoglossum maxillingua		X	
Hybognathus hankinsoni		X	
Hybognathus nuchalis		X	
Nocomis biguttatus		X	
Notemigonus crysoleucas	X	X	X
Notropis amoenus		X	
Notropis analostanus		X	
Notropis atherinoides	X	X	
Notropis bifrenatus		X	
Notropis chalybaeus		X	
Notropis cornutus	X	X	X
Notropis heterodon			
Notropis heterolepis		X	
Notropis hudsonius	X	X	
Notropis rubellus		X	
Notropis spilopterus		X	
Notropis stramineus		X	
Notropis volucellus	X	X	
Phoxinus eos		X	X
Phoxinus neogaeus		X	X
Pimephales notatus	X	X	
Pimephales promelas		X	
Rhinichthys atratulus		X	X
Rhinichthys cataractae		X	
Rhodeus sericeus		X	
Scardinius erythrophthalmus		X	
Semotilus atromaculatus		X	X
Semotilus corporalis		X	X
Semotilus margarita		X	X
CATOSTOMIDAE			
Catostomus catostomus		X	
Catostomus commersoni	X	X	X
Erimyzon oblongus		X	
Hypentelium nigricans	X	X	
Moxostoma macrolepidotum		X	
Moxostoma valenciennesi	X		
ICTALURIDAE			
Ictalurus catus		X	
Ictalurus melas		X	
Ictalurus natalis		X	
Ictalurus nebulosus	X	X	X
Ictalurus punctatus	X	X	
Noturus flavus		X	
Noturus gyrinus		X	
Noturus insignis		X	
PERCOPSIDAE			
Percopsis omiscomaycus	X	X	
GADIDAE			
Lota lota	X		
Microgadus tomcod			X
CYPRINODONTIDAE			
Cyprinodon diaphanus		X	
Fundulus variegatus		X	X
Fundulus heteroclitus		X	X
ATHERINIDAE			
Labidesthes sicculus		X	
GASTEROSTEIDAE			
Apeltes quadracus		X	
Culaea inconstans		X	X
Gasterosteus aculeatus	X	X	X
Pungitius pungitius		X	X
PERCICHTHYIDAE			
Morone americana	X	X	X
Morone chrysops	X	X	
Morone saxatilis		X	X
CENTRARCHIDAE			
Acantharchus pomotis		X	
Ambloplites rupestris	X	X	
Enneacanthus gloriosus		X	
Enneacanthus obesus		X	
Lepomis auritus		X	
Lepomis cyanellus		X	
Lepomis gibbosus	X	X	
Lepomis gulosus		X	
Lepomis macrochirus	X	X	
Micropterus dolomieui	X	X	
Micropterus salmoides	X	X	
Pomoxis annularis		X	

North America Atlantic Drainage rivers	Laurentian Great Lakes (Edwards et al. 1989)	Hudson (Limburg et al. 1989)	Miramichi (Randall et al. 1989)
Pomoxis nigromaculatus		X	
PERCIDAE			
Etheostoma blennioides		X	
Etheostoma flabellare		X	
Etheostoma nigrum	X	X	
Etheostoma olmstedi		X	
Perca flavescens	X	X	X
Percina caprodes	X	X	
Percina peltata		X	
Stizostedion vitreum	X	X	
CARANGIDAE			
Decapterus macarellus		X	
SCIAENIDAE			
Aplodinotus grunniens	X		
POLYNEMIDAE			
Polydactylus octonemus		X	
ELEOTRIDAE			
Dormitator maculatus		X	
COTTIDAE			
Cottus bairdi	X		
Cottus cognatus		X	X
Myoxocephalus aenaeus		X	

North America Mississippi River Drainage	Mississippi (Fremling et al. 1989)	Missouri (Hesse et al. 1989)	Tennessee (Voigtlander and Poppe 1989)
PETROMYZONTIDAE			
Ichthyomyzon castaneus	X	X	
Ichthyomyzon fossor		X	
Ichthyomyzon gagei	X	X	
Ichthyomyzon unicuspis	X	X	
CARCHARHINIDAE			
Carcharhinus leucas	X		
DASYATIDAE			
Dasyatis sabina	X		
Dasyatis sayi	X		
ACIPENSERIDAE			
Acipenser fulvescens	X	X	
Acipenser oxyrhynchus	X		
Scaphirhynchus albus	X	X	
Scaphirhynchus platorynchus	X	X	
POLYODONTIDAE			
Polydon spathula	X	X	X
LEPISOSTEIDAE			
Lepisosteus oculatus	X		
Lepisosteus osseus	X	X	
Lepisosteus platostomus	X	X	
Lepisosteus spatula	X		
AMIIDAE			
Amia calva	X	X	
ELOPIDAE			
Elops saurus	X		
Megalops atlanticus	X		
ANGUILLIDAE			
Anguilla rostrata	X	X	
OPHICHTHIDAE			
Myrophis punctatus	X		
CLUPEIDAE			
Alosa alabamae	X	X	
Alosa chrysochloris	X	X	
Alosa pseudoharengus		X	X
Brevoortia patronus	X		
Dorosoma cepedianum		X	X
Dorosoma petense	X	X	X
ENGRAULIDAE			
Ancho mitchilli	X		
HIODONTIDAE			
Hiodon alosoides	X	X	
Hiodon tergisus	X	X	
SALMONIDAE			
Coregonus artedii	X	X	X
Coregonus clupeaformis	X	X	

North America Mississippi River Drainage	Mississippi (Fremling et al. 1989)	Missouri (Hesse et al. 1989)	Tennessee (Voigtlander and Poppe 1989)
Oncorhynchus kisutch		X	
Oncorhynchus nerka		X	X
Oncorhynchus tshawytscha		X	
Prosopium gemmiferum		X	
Prosopium williamsoni		X	
Salmo aguabonita		X	
Salmo clarki		X	X
Salmo gairdneri	X	X	X
Salmo trutta		X	X
Salvelinus fontinalis	X	X	X
Salvelinus namaycush		X	X
Thymallus arcticus		X	
OSMERIDAE			
Osmerus mordax	X	X	X
UMBRIDAE			
Umbra limi	X		
ESOCIDAE			
Esox americanus vermiculatus		X	
Esox lucius	X	X	X
Esox masquinongy	X	X	X
Esox niger	X		
CYPRINIDAE			
Campostoma anomalum	X	X	
Campostoma oligolepis		X	
Carassius auratus	X	X	
Couesius plumbeus		X	
Ctenopharyngodon idella	X	X	X
Cyprinus carpio	X	X	X
Ericymba buccata	X		
Gila atraria		X	
Hybognathus argyritis	X		
Hybognathus hankinsoni	X	X	
Hybognathus hayi	X		
Hybognathus nuchalis	X	X	
Hybognathus placitus	X	X	
Hybopsis aestivalis	X	X	
Hybopsis gelida	X	X	
Hybopsis gracilis	X	X	
Hybopsis meeki		X	
Hybopsis storeriana	X	X	
Hybopsis winchelli (amblops)	X		
Hybopsis x-punctata	X	X	
Nocomis biguttatus	X	X	
Nocomis leptocephalus	X		
Notemigonus crysoleucas	X	X	
Notropis amnis	X		
Notropis anogenus	X		
Notropis atherinoides	X	X	
Notropis atrocaudalis	X		
Notropis bairdi	X		
Notropis blennius	X	X	
Notropis boops	X	X	
Notropis buchanani	X	X	
Notropis camurus	X		
Notropis chalybaeus	X		
Notropis chrysocephalus	X	X	
Notropis cornutus	X	X	
Notropis dorsalis	X	X	
Notropis emiliae	X	X	
Notropis fumeus	X		
Notropis greenei		X	
Notropis heterodon	X		
Notropis heterolepis	X	X	
Notropis hubbsi	X		
Notropis hudsonius	X	X	
Notropis longirostris	X		
Notropis lutrensis	X	X	
Notropis maculatus	X		
Notropis nubilus	X	X	
Notropis potteri	X		
Notropis rubellus	X	X	
Notropis shumardi	X	X	
Notropis spilopterus	X	X	
Notropis stilbius	X	X	
Notropis stramineus	X	X	
Notropis texanus	X		
Notropis topeka		X	
Notropis umbratilis		X	
Notropis venustus	X		
Notropis volucellus	X	X	
Notropis whipplei	X		
Notropis zonatus		X	
Phenacobius mirabilis	X	X	
Phoxinus eos	X	X	
Phoxinus erythrogaster	X	X	
Phoxinus neogaeus	X	X	
CATOSTOMIDAE			
Carpiodes carpio	X	X	
Carpiodes cyprinus	X	X	
Carpiodes velifer	X	X	
Catostomus commersoni	X	X	
Catostomus catostomus		X	
Catostomus platyrhynchus		X	
Cycleptus elongatus	X	X	
Erimyzon oblongus	X		
Erimyzon succetta	X		

North America Mississippi River Drainage	Mississippi (Fremling et al. 1989)	Missouri (Hesse et al. 1989)	Tennessee (Voigtlander and Poppe 1989)
Hypentelium nigricans	X	X	
Ictiobus bubalus	X	X	
Ictiobus cyprinellus	X	X	
Ictiobus niger	X	X	
Ictiobus sp.			X
Minytrema melanops	X	X	X
Moxostoma anisurum	X	X	
Moxostoma carinatum	X	X	
Moxostoma duquesnei		X	
Moxostoma erythrurum	X	X	
Moxostoma macrolepidotum	X	X	
Moxostoma poecilurum	X		
Moxostoma valenciennesi	X		
ICTALURIDAE			
Ictalurus catus	X		
Ictalurus furcatus	X	X	
Ictalurus melas	X	X	
Ictalurus natalis	X		
Ictalurus nebulosus	X		
Ictalurus punctatus	X	X	
Ictalurus sp.			X
Noturus eleutherus	X		
Noturus exilis		X	
Noturus flavus	X	X	
Noturus gyrinus	X	X	
Noturus leptacanthus	X		
Noturus nocturnus	X	X	
Noturus phaeus	X		
Noturus stigmosus	X		
Pylodictis olivaris	X	X	
ARIIDAE			
Arius felis	X		
Bagre marinus	X		
AMBLYOPSIDAE			
Amblyopsis rosae		X	
Typhlichthys subterraneus		X	
APHREDODERIDAE			
Aphredoderus sayanus	X		
PERCOPSIDAE			
Percopsis omiscomaycus	X	X	
GADIDAE			
Lota lota	X	X	
BELONIDAE			
Strongylura marina	X		
CYPRINODONTIDAE			
Cyprinodon variegatus	X		
Fundulus catenatus	X	X	
Fundulus chrysotus	X		
Fundulus diaphanus		X	
Fundulus grandis	X		
Fundulus jenkinsi	X		
Fundulus kansae		X	
Fundulus notatus	X	X	
Fundulus notti	X		
Fundulus olivaceus	X	X	
Fundulus sciadicus		X	
Lucania parva	X		
POECILIIDAE			
Gambusia affinis	X	X	
Heterandria formosa	X		
Poecilia latipinna	X		
ATHERINIDAE			
Labidesthes sicculus	X	X	
Membras martinica	X		
Menidia beryllina	X		
Menidia peninsulae	X		
GASTEROSTEIDAE			
Culaea inconstans	X	X	
Pungitius pungitius	X		
SYNGNATHIDAE			
Syngnathus scovelli	X		
PERCICHTHYIDAE			
Morone americana		X	
Morone chrysops	X	X	X
Morone mississippiensis	X	X	
Morone saxatilis	X	X	X
CENTRARCHIDAE			
Ambloplites ariommus	X		
Ambloplites rupestris	X	X	
Archoplites interruptus		X	
Centrarchus macropterus	X		
Elassoma zonatum	X		
Lepomis cyanellus	X	X	
Lepomis gibbosus	X	X	
Lepomis gulosus	X	X	
Lepomis humilis	X	X	
Lepomis macrochirus	X	X	
Lepomis marginatus	X		
Lepomis megalotis	X	X	
Lepomis microlophus	X		
Lepomis punctatus	X		
Lepomis symmetricus	X		
Lepomis sp.			X

North America Mississippi River Drainage	Mississippi (Fremling et al. 1989)	Missouri (Hesse et al. 1989)	Tennessee (Voigtlander and Poppe 1989)
Micropterus dolomieui	X	X	
Micropterus punctulatus	X	X	
Micropterus salmoides	X	X	X
Micropterus sp.			X
Pomoxis annularis	X	X	
Pomoxis nigromaculatus	X	X	
Pomoxis sp.			X
PERCIDAE			
Ammocrypta asprella	X	X	
Ammocrypta clara	X		
Ammocrypta vivax	X		
Etheostoma asprigene	X		
Etheostoma blennioides		X	
Etheostoma caeruleum	X	X	
Etheostoma chlorosomum	X		
Etheostoma exile	X	X	
Etheostoma flabellare	X	X	
Etheostoma fusiforme	X		
Etheostoma gracile	X	X	
Etheostoma microperca	X	X	
Etheostoma nianguae		X	
Etheostoma nigrum	X	X	
Etheostoma parvipinne	X		
Etheostoma proeliare	X		
Etheostoma punctulatus		X	
Etheostoma spectabile	X	X	
Etheostoma swaini	X		
Etheostoma tetrazonum		X	
Etheostoma whipplei	X		
Etheostoma zonale	X	X	
Perca flavescens	X	X	X
Percina caprodes	X	X	
Percina copelandi	X		
Percina cymatotaenia		X	
Percina evides	X	X	
Percina maculata	X	X	
Percina ouachitae	X		
Percina phoxocephala	X	X	
Percina sciera	X		
Percina shumardi	X	X	
Percina tanasi			X

North America Mississippi River Drainage	Mississippi (Fremling et al. 1989)	Missouri (Hesse et al. 1989)	Tennessee (Voigtlander and Poppe 1989)
Percina uranidea	X		
Stizostedion canadense	X	X	X
Stizostedion vitreum vitreum	X	X	X
CARANGIDAE			
Caranx hippos	X		
Caranx latus	X		
Oligoplites saurus	X		
LUTJANIDAE			
Lutjanus griseus	X		
GEREIDAE			
Gerres cinereus	X		
SPARIDAE			
Archosargus probatocephalus	X		
Lagodon rhomboides	X		
SCIAENIDAE			
Aplodinotus grunniens	X	X	X
Bairdiella chrysoura	X		
Cynoscion arenarius	X		
Cynoscion nebulosus	X		
Cynoscion nothus	X		
Leiostomus xanthurus	X		
Menticirrhus littoralis	X		
Micropogonias undulatus	X		
Pogonias cromis	X		
Sciaenops ocellatus	X		
CICHLIDAE			
Tilapia mossambica	X		
MUGILIDAE			
Mugil cephalus	X		
Mugil curema	X		
ELEOTRIDAE			
Dormitator maculatus	X		
Eleotris pisonis	X		
GOBIIDAE			
Evorthodus lyricus	X		
Gobioides broussoneti	X		
Gobionellus boleosoma	X		
Gobionellus hastatus	X		
Gobionellus shufeldti	X		
Gobionellus stigmaturus	X		
Gobiosoma bosci	X		
Microgobius gulosus	X		

North America Mississippi River Drainage	Mississippi (Fremling et al. 1989)	Missouri (Hesse et al. 1989)	Tennessee (Voigtlander and Poppe 1989)
SCOMBRIDAE			
Scomberomorus maculatus	X		
COTTIDAE			
Cottus bairdi	X	X	
Cottus carolinae	X	X	
BOTHIDAE			
Citharichthys spilopterus	X		
Etropus crossotus	X		
Paralichthys lethostigma	X		
SOLEIDAE			
Achirus lineatus	X		
Trinectes maculatus	X		
CYNOGLOSSIDAE			
Symphurus plagiusa	X		

South American Rivers	Amazon (Bayley and Petrere 1989)	Magdalena (Valderrama and Zarate 1989)	Orinoco (Novoa 1989)	Plata (Quirós 1989)
CARCHARHINIDAE	X			
PRISTIDAE	X			
POTAMOTRYGONIDAE	X			
Potamotrygon magdalenae		X		
LEPIDOSIRENIDAE	X			
OSTEOGLOSSIDAE				
Arapaima gigas	X			
Osteoglossum bicirrhosum	X			
MEGALOPIDAE				
Tarpon atlanticus		X		
CLUPEIDAE		X		
Pellona flavipinnis			X	
Pellona sp.	X			
ENGRAULIDIDAE	X			
Lycengraulis olidus				X
CYPRINIDAE	X			
HEMIODONTIDAE				
Anodus melanopogon	X			
Hemiodus microlepis	X			
CURIMATIDAE				
Curimata mivartii		X		
Curimata sp.	X			
Cyrtocharax magdalenae		X		
Eigenmannina virescens		X		
Potamorhina pristigaster	X			
Prochilodus mariae			X	
Prochilodus nigricans	X			
Prochilodus platensis		X		X
Prochilodus reticulatus		X		
Semaprochilodus insignis	X			
Semaprochilodus kneri			X	
Semaprochilodus laticeps			X	
Semaprochilodus taeniatus	X			
ANOSTOMIDAE				
Leporinus muyscorum		X		
Leporinus obtusidens				X
Leporinus sp.	X			
Rhytiodus sp.	X			
Schizodon fasciatum	X			

South American Rivers	Amazon (Bayley and Petrere 1989)	Magdalena (Valderrama and Zarate 1989)	Orinoco (Novoa 1989)	Plata (Quirós 1989)
ERYTHRINIDAE				
Hoplias malabaricus	X	X	X	X
CHARACIDAE				
Astyanax sp.		X		
Brycon melanopterus	X			
Brycon moorei		X		
Brycon orbignyanus				X
Hydrolycus scomberoides			X	
Paracheirodon axelrodi	X			
Roeboides dayi		X		
Salminus affinis		X		
Salminus maxillosus				X
Triportheus elongatus			X	
Triportheus magdalenae		X		
Triportheus sp.	X			
SERRASALMIDAE (CHARACIDAE)				
Colossoma macropomum	X		X	
Colossoma mitrei				X
Colossoma sp.		X		
Metynnis sp.	X			
Myleus sp.	X			
Myloplus sp.	X			
Mylossoma duriventris			X	
Mylossoma sp.	X			
Piaractus brachypomus	X		X	
Pygocentrus sp.	X			
Serrasalmus sp.	X			
ARIIDAE				
Arius parkeri	X			
Cynoscion sp.	X			
DORADIDAE				
Lithodoras dorsalis	X			
Megalodoras irwini			X	
Megalodoras sp.	X			
Oxydoras kneri				X
Oxydoras niger	X		X	
Pterodoras angelli			X	
Pterodoras granulosus				X
Pterodoras sp.	X			
AUCHENIPTERIDAE				
Trachycorystes insignis		X		
PIMELODIDAE				
Brachyplatystoma filamentosum	X			
Brachyplatystoma flavicans	X			
Brachyplatystoma vaillantii	X		X	
Luciopimelodus pati				X
Parapimelodus valenciennensi				X
Phractocephalus hemioliopterus	X		X	
Pimelodella sp.				X
Pimelodus albicans				X
Pimelodus clarias		X		X
Pimelodus fasciatus		X		
Pseudopimelodus zungaro				X
Pseudoplatystoma coruscans				X
Pseudoplatystoma fasciatum	X	X	X	X
Pseudoplatystoma tigrinum	X		X	
Sorubim lima		X		X
Sorubim limacurimata magdalenae		X		
AGENEIOSIDAE				
Ageneiosus caucanus		X		
Ageneiosus sp.				X
HYPOPHTHALMIDAE				
Hypophthalmus sp.	X			
CALLICHTHYIDAE				
Hoplosternum littoralle			X	
LORICARIIDAE				
Hypostomus sp.			X	
Loricaria filamentosa		X		
Plecostomus sp.	X			
Pterygoplichthys undecimalis		X		
Pterygoplichthys sp.	X			
RHAMPHICHTHYIDAE				
Sternopygus macrurus		X		
SALMONIDAE				
Salmo gairdneri		X		
CYPRINIDONTIDAE	X			
POECILIIDAE	X			
SYNBRANCHIDAE	X			
CARANGIDAE	X			
SCIAENIDAE				
Plagioscion montei	X			
Plagioscion squamosissimus	X		X	
Plagioscion surinamensis		X		
NANDIDAE	X			

South American Rivers	Amazon (Bayley and Petrere 1989)	Magdalena (Valderrama and Zarate 1989)	Orinoco (Novoa 1989)	Plata (Quirós 1989)
CICHLIDAE				
Astronotus ocellatus	X		X	
Chaetobranchus sp.	X			
Cichla ocellaris	X		X	
Cichla temensis	X			
Cichlasoma sp.	X			
Geophagus sp.	X			
Oreochromis niloticus		X		
Petenia kraussi	X	X		
Symphysodon sp.	X			
Uaru sp.	X			
GYMNOTIDAE			X	
GOBIIDAE	X			
TETRAODONTIDAE	X			

European and USSR Rivers	British rivers (Mann 1989)	Danube (Bacalbasa-Dobrovici 1989)	Rhine (Lelek 1989)	Vistula (Backiel and Penczak 1989)	Volga (Pavlov and Vilenkin 1989)
PETROMYZONTIDAE					
Lampetra fluviatilis			X		
Lampetra planeri			X		
Petromyzon marinus			X		
ACIPENSERIDAE					
Acipenser guldenstaedti		X			X
Acipenser nudiventris		X			X
Acipenser ruthenus		X			X
Acipenser stellatus		X			X
Acipenser sturio		X	X	X	
Huso huso		X			X
ANGUILLIDAE					
Anguilla anguilla	X	X	X	X	X
CLUPEIDAE					
Alosa alosa	X		X		
Alosa caspia		X			
Alosa fallax	X		X		
Alosa pontica		X			
Caspialosa brashnikovi					X
Caspialosa caspia					X
Caspialosa kessleri					X
Clupeonella cultriventris		X			
Clupeonella delicatula					X
SALMONIDAE					
Coregonus albula ladogensis					X
Coregonus artedii					X
Coregonus lavaretus		X			X
Coregonus oxyrhynchus			X		
Coregonus peled		X			X
Hucho hucho		X	X		
Oncorhynchus tshawytscha			X		
Salmo gairdneri		X	X		
Salmo salar	X		X	X	

European and USSR Rivers	British rivers (Mann 1989)	Danube (Bacalbasa-Dobrovici 1989)	Rhine (Lelek 1989)	Vistula (Backiel and Penczak 1989)	Volga (Pavlov and Vilenkin 1989)
Salmo trutta		X	X	X	X
Salvelinus alpinus			X		
Salvelinus fontinalis		X	X		
Stenodus leucichthys					X
Stenodus stenodus					X
Thymallus thymallus	X	X	X		
OSMERIDAE					
Osmerus eperlanus	X		X		X
ESOCIDAE					
Esox lucius	X	X	X	X	X
CYPRINIDAE					
Abramis ballerus		X			X
Abramis brama	X	X	X	X	X
Abramis sapa		X			X
Alburnoides bipunctatus			X		
Alburnus alburnus	X	X	X	X	X
Aristichthys nobilis		X			X
Aspius aspius		X	X	X	X
Barbus barbus	X	X	X	X	
Blicca bjoerkna		X	X	X	X
Carassius auratus		X	X		X
Carassius carassius		X	X		X
Chondrostoma nasus		X	X	X	X
Ctenopharyngodon idella		X	X		X
Cyprinus carpio	X	X	X		X
Gobio gobio	X		X	X	X
Hypophthalmichthys molitrix		X	X		X
Leucaspius delineatus			X		X
Leuciscus cephalus	X	X	X	X	X
Leuciscus idus		X	X	X	X
Leuciscus leuciscus	X			X	X
Leuciscus souffia			X		
Pelecus cultratus		X		X	X
Phoxinus phoxinus			X		X
Pseudorasbora parva		X	X		
Rhodeus sericeus amarus			X	X	
Rutilus rutilus	X	X	X	X	X
Scardinius erythrophthalmus		X	X		X
Tinca tinca		X	X		X
Vimba vimba		X	X	X	
CATOSTOMIDAE					
Ictiobus bubalus		X			
Ictiobus cyprinellus		X			
Ictiobus niger		X			
COBITIDAE					
Cobitis taenia			X		X
Misgurnus fossilis		X	X		X
Noemacheilus barbatulus			X		
ICTALURIDAE					
Ictalurus nebulosus		X	X		
SILURIDAE					
Silurus glanis		X	X	X	X
GADIDAE					
Lota lota			X	X	X
ATHERINIDAE					
Atherina boyeri pontica		X			
GASTEROSTEIDAE					
Gasterosteus aculeatus		X	X		
Pungitius pungitius			X		
CENTRARCHIDAE					
Lepomis gibbosus		X	X		
Micropterus dolomieui		X			
Micropterus salmoides			X		
PERCIDAE					
Gymnocephalus cernua			X		X
Perca fluviatilis	X	X	X	X	X
Stizostedion lucioperca		X	X	X	X
Stizostedion volgensis					X
Zingel streber		X			
Zingel zingel		X			
CICHLIDAE					
Astronotus ocellatus			X		
GOBIIDAE					
Proterorhynus marmoratus		X			

European and USSR Rivers	British rivers (Mann 1989)	Danube (Bacalbasa-Dobrovici 1989)	Rhine (Lelek 1989)	Vistula (Backiel and Penczak 1989)	Volga (Pavlov and Vilenkin 1989)
COTTIDAE					
Cottus gobio			X	X	X
PLEURONECTIDAE					
Platichthys flesus			X		

Africa	African rivers (Welcome 1989)	Niger (Malvestuto and Meredith 1989)
PROTOPTERIDAE		
Protopterus sp.	X	
POLYPTERIDAE		
Polypterus senegalus	X	
OSTEOGLOSSIDAE		
Heterotis niloticus	X	
PANTODONTIDAE		
Pantodon buchholzi	X	
MORMYRIDAE		
Campylomormyrus tamandua		X
Hyperopisus bebe occidentalis		X
Marcussenius senegalensis pfaffi		X
Mormyrops sp.		X
Mormyrus rume		X
GYMNARCHIDAE		
Gymnarchus sp.	X	
CYPRINIDAE		
Barbus lorenzi	X	
Barbus occidentalis	X	
Labeo coubie	X	X
Labeo senegalensis	X	X
CITHARINIDAE		
Citharinus citharus	X	X
Citharinus distichodoides	X	
Citharinus latus	X	
CHARACIDAE		
Alestes leuciscus	X	
Alestes baremoze	X	X
Alestes dentex	X	X
Alestes nurse		X
Hepsetus sp.	X	
Hydrocynus brevis	X	
Hydrocynus forskalii	X	
BAGRIDAE		
Auchenoglanis sp.		X
Bagrus bajad		X
Bagrus docmak		X
Chrysichthys auratus longifilis		X
Chrysichthys nigrodigitatus		X
SCHILBEIDAE		
Schilbe mystus		X
Schilbe niloticus		X
CLARIIDAE		
Clarias anguillaris		X
Heterobranchus bidorsalis		X
MOCHOKIDAE		
Hemisynodontis membranaceous		X
Synodontis schall		X
Synodontis violaceus		X

Africa	African rivers (Welcome 1989)	Niger (Malvestuto and Meredith 1989)
CENTROPOMIDAE		
Lates niloticus	X	X
CICHLIDAE		
Oreochromis andersoni	X	
Oreochromis macrochir	X	
Oreochromis niloticus		X
Sarotherodon galilaeus		X
Tilapia rendalli	X	X
Tilapia zillii		X

India Ganga River (Natarajan 1989)
NOTOPTERIDAE
Notopterus chitala (Featherback)
Notopterus notopterus
CLUPEIDAE
Hilso ilisha (Hilsa)
ENGRAULIDIDAE
Setipinna phasa (Engraulis telara)
CYPRINIDAE
Amblypharyngodon mola
Aspidoparia morar
Catla catla
Chela laubuca
Cirrhina mrigala
Cirrhina reba
Labeo bata
Labeo boga
Labeo calbasu
Labeo dero
Labeo dyocheilus
Labeo gonius
Labeo rohita
Oxygaster bacaila
Puntius sarana sarana
Schizothoraichthys (Schizothorax) progastus
Schizothorax kumzonensis
Tor (Barbus) putitora
Tor (Barbus) tor
PSILORHYNCHIDAE
HOMALOPTERIDAE
COBITIDIDAE
BAGRIDAE
Clarias batrachus
SILURIDAE
Ailia coila
Ailiichthys punctata
Clupisoma (Pseudeutropius) garua
Eutropiichthys vacha
Gagata cenia
Mystus (Macrones) aor
Mystus (Macrones) cavasius
Mystus (Macrones) seenghala
Mystus (Macrones) sp.
Ompok bimaculatus
Ompok pabda
Rita rita (R. buchanani)
Wallago attu
PANGASIIDAE
Pangasius pangasius
Silonia silondia
SISORIDAE
Bagarius bagarius
HETEROPNEUSTIDAE
Heteropneustes fossilis
SYNBRANCHIDAE
MUGILIDAE
Mugil corsula

India
Ganga River
(Natarajan 1989)

GOBIIDAE
Glossogobius (Gobius) gutum

ANABANTIDAE
Anabas testudineus

CHANNIDAE
Channa marulius
Channa striatus

MASTACEMBELIDAE
Macrognathus aculeatus
Mastacembelus armatus
Mastacembelus pancalus

China
Pearl River
(Liao et al. 1989)

ACIPENSERIDAE
Acipenser sinensis (Chinese sturgeon)

ANGUILLIDAE
Anguilla japonica (Japanese eel)
Anguilla mauritiana (Spotted eel)

CLUPEIDAE
Clupanodon thrissa (gizzard shad)
Clupea (Macrura) reevesii (Chinese shad)
Salanx sp.

ENGRAULIDIDAE
Coilia grayi (C. nasus)
Coilia mystus

CYPRINIDAE
Anabarilius qujingensis
Aristichthys nobilis (bighead carp)
Barbodes caldwelli
Barbodes denticulatus denticulatus
Barbodes denticulatus yunnanensis
Barbodes lacustris
Carassius auratus auratus (crucian carp)
Carassoides cantonensis (barbelled carp)
Cirrhinus molitorella (mud carp)
Ctenopharyngodon idella (grass carp)
Cyprinus carpio haematopterus (common carp)
Elopichthys bambusa (false salmon)
Erythroculter hypselonotus
Erythroculter pseudobrevicauda
Garra pingi yiliangensis
Hemibarbus labeo
Hemibarbus maculatus
Hemiculter leucisculus
Hypophthalmichthys molitrix (silver carp)
Labeo rohita
Megalobrama hoffmanni (Guangdong bream)
Mylopharyngodon piceus (black carp)
Ochetobius elongatus (tube fish)
Parabramis pekinensis (Peking bream)
Ptychidio jordani (mouse fish)
Ptychidio macrops
Saurogobio dabryi
Semilabeo notabilis (lip fish)
Sinilabeo decorus decorus
Sinocyclocheilus grahami tingi
Sinocyclocheilus grahami vangzongensis
Sinocyclocheilus guilinensis
Squaliobarbus curriculus (eastern barbel)
Tor (Barbus) brevibilis brevibilis
Varicorhinus (Onychostoma) gerlachi
Varicorhinus (Onychostoma) lini
Xenocypris argentea

COBITIDIDAE

HOMALOPTERIDAE

BAGRIDAE
Mystus (Hemibagrus) guttatus
Pseudobagrus fulvidraco

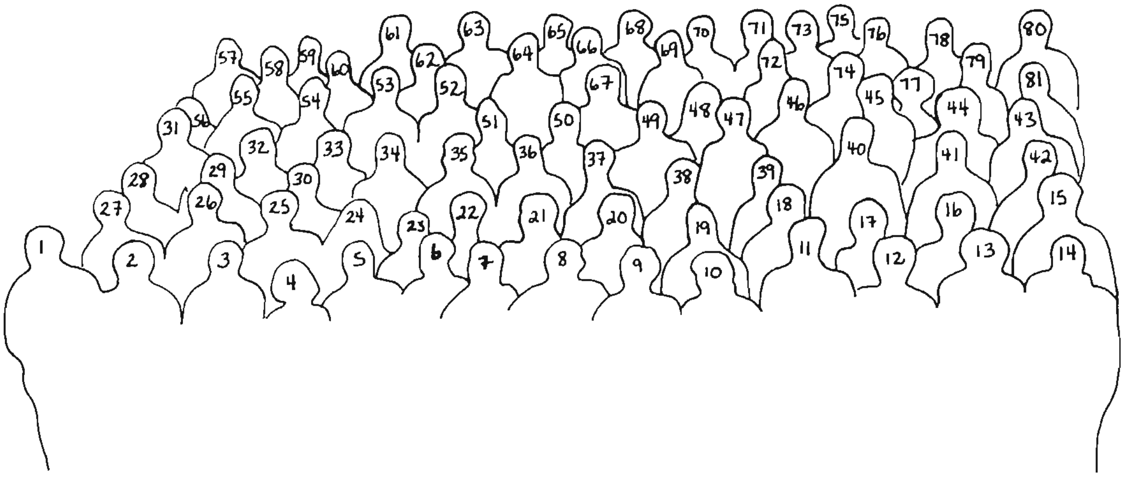
CRANOGLANIDIDAE
Cranoglanis sinensis

SILURIDAE
Silurus asotus

China Pearl River (Liao et al. 1989)
CLARIIDAE *Clarias fuscus*
ARIIDAE *Arius sinensis*
SERRANIDAE *Lateolabrax japonicus* (perch) *Siniperca knerii* (mandarin fish)
SPARIDAE *Sparus latus*
SCIAENIDAE *Collichthys lucidus*
MUGILIDAE *Mugil cephalus* (grey mullet)
GOBIIDAE *Odontamblyopus rubicundus* *Parapocryptes serperaster* *Periophthalmus cantonensis* *Taenioides anguillaris*
BELONTIIDAE *Ophicephalus maculatus* (snake fish)
CYNOGLOSSIDAE *Cynoglossus trigramus* (tongue sole)

List of LARS Participants

(Numbers preceding participants' names refer to the key of the photograph; an asterisk precedes names of participants not in the photograph.)



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